An Investigation of the Prerequisite Conditions which Enable Invasion of Moist Grasslands by *Dalbergia obovata*

By

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As the candidate's supervisors we have approved this dissertation for submission.

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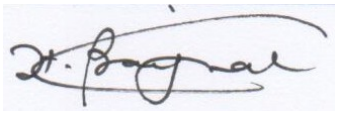
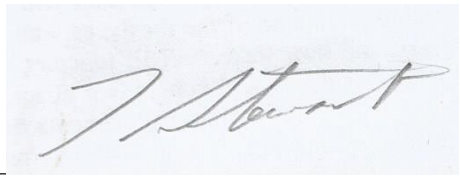
Signed:  Name: ___Himansu Baijnath_____ Date: ___2019.03.08____

PREFACE

The research contained in this dissertation was completed by the candidate while based in the Discipline of Biology, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville, South Africa.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate under the supervision of Professors Peter Scogings and Himansu Baijnath. .

The structure of the dissertation is in the form of papers for publication and therefore necessitates some repetition as well as some variation among the chapters.



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DECLARATION 1: PLAGIARISM

I, Terry Stewart, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material, prepared by myself, published as journal articles or presented as a poster and oral presentations at conferences. In some cases, additional material has been included;

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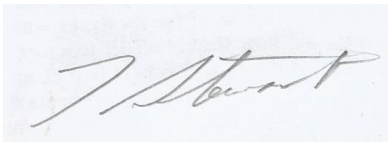
3 

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DECLARATION 2: PUBLICATIONS

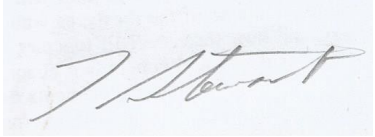
My role in each paper and presentation is indicated. The * indicates corresponding author. For each paper, I conceived the idea, developed the methods, collected and analysed the data, and led most of the writing. My co-authors guided the overall conceptualisation of the work and contributed editorially to the writing.

Chapter 2

Stewart T*, Scogings PF and Baijnath H., An investigation of the encroachment of sub-tropical moist coast grasslands within the urban nature reserves of Ethekwini Municipality by *Dalbergia obovata*, an indigenous forest liana. Submitted to *Bothalia: African Biodiversity and Conservation* on 2nd December 2018. The paper presents the results of the analysis of reserve management records and field mapping surveys for the distribution of *D. obovata* in the grasslands of nature reserves within Ethekwini Municipality and concludes that *D. obovata* has encroached into the moist coast grasslands.

Chapter 3

Stewart T*, Scogings PF and Baijnath H. An assessment of the distribution of *Dalbergia obovata* diaspores from forest margins and post establishment vegetative propagation within adjacent grasslands. Submitted to *Bothalia: African Biodiversity and Conservation* on 16th December 2018. Using a simplified wind dispersal model and analysis of historical changes in distinct stands in grasslands it was concluded that successful establishments were infrequent and that clonal propagation was the primary mechanism for expansion of plants.



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ABSTRACT

Encroachment by *Dalbergia obovata* into moist coastal grasslands within eThekwini Municipality was identified as a potential threat to the conservation of this threatened habitat type. An investigation was undertaken to confirmation whether or not D. *obovata* was in fact encroaching into the city's grasslands and to identify the probable underlying drivers and local factors that contributed to encroachment. The investigation comprised four areas of focus. The first was an assessment of the management practices and records of *D. obovata* encroachment extracted from the available reserve management records of seventeen nature reserves and conservation areas. The summarised data from the records was then processed using a Chi-square test and Principal Components Analysis. The second phase focussed on the application of field surveys to record the distribution patterns of *D. obovata* within four selected management areas. The results were then captured in a GIS map against which the results of the Chi-square and PCA tests were compared. In phase three a simple theoretical ballistics model was developed from experimental data to predict the anomochoric distribution of *D. obovata* diaspores from the forest into adjacent grasslands and the critical positioning of parent plants in the host trees in relation to the edge of the canopy. The final focal area involved the mapping of individual plants within stands of *D. obovata* and comparison against sixteen years of historical orthophoto records in order to determine the historic patterns and rates at which *D. obovata* became established and propagated within the grasslands. During this part of the investigation the vegetative propagation of *D. obovata* by clonal propagation from lateral branches and roots was identified and which provided an explanation of how *D. obovata* was able to form large dense stands with no evidence of canopy contact mortality. The final conclusions were that *D. obovata* parent plants had to be positioned on the edge of the forest canopy for diaspores to successfully escape the canopy, that successful establishment of *D. obovata* in grasslands from any particular parent plant was infrequent and that *D. obovata* did not become established in the presence of large mixed feeder herbivores. However once established in the grasslands, the ability to spread via clonal propagation enabled *D. obovata* to both outcompete grass species for available resources and be resilient to conventional bush encroachment management practices which relied on controlled burning programs.

ACKNOWLEDGEMENTS

The author wishes to acknowledge the following people for their continual encouragement and support. My brother Clive Stewart, my mother Mrs Yvonne Stewart and Mark Hodgetts my life long friend

Gratitude is also extended to the following members of my work colleagues and staff of the Natural Resources management Division of the eThekwini Municipality Parks, Liesure and Cemeteries Department for their assistance with the collection of field data and the provision of management records, Kenneth L Mabila, Philip J Zuma, Nicholas Liebenberg, Thami Kunene, Jabulani Khoza, Christopher Ngcobo and Zethu Gumede. Acknowledgement is also given to the staff of the Environmental Planning and Climate Protection Department of eThekwini Municipality as well as the Reserve Managers and staff of the Scientific Services Department of Ezemvelo KZN Wildlife for access to the reserve management records and nature reserves under their management.

Special acknowledgement is given to Dr D Roberts for her pivotal role in motivating for this research project to be considered for a post graduate study through the Durban Research Action Partnership between Ethekwini Municipality and the University of KwaZulu-Natal and finally to Professor Peter F Scogings and Professor Himansu Baijnath my supervisors at UKZN for their continual guidance and patience during this post graduate research.

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CHAPTER 1: **Introduction**

1.1 Rationale for the research

The City of Durban (eThekwini Municipality) is situated within the approximate centre of the Maputuland – Pondoland – Albany biome which is recognised as a global biodiversity hotspot (Boon et al.,2016). Approximately nine percent or 2267 of the total indigenous plant species for South Africa (McLean C., 2016) have been recorded within the Municipal boundaries with a large percentage of them occurring within grassland ecosystems. These grasslands were identified as Kwazulu-Natal Sandstone Sourveld which is separated by an escarpment at approximately 400m – 450m (Boon, 2017), into an inland region and a coastal belt with a mean annual precipitation (MAP) of 819 mm to 1272 mm (Mucina et al., 2006). These coastal grasslands therefore fall into the category of wet, moist or mesic grasslands (Devine et al., 2017) which tend to be unstable grasslands (Sankaran et al., 2005) comprising both grass and woody components, the proportional representation of which is influenced by a number of local conditions including the frequency and intensity of fires (Govender et al., 2006, Joubert et al., 2012, Devine et al., 2017). Moist coastal grasslands are also listed as the most threatened of the South African grassland ecosystems (Cadman et al., 2013) with less than 8% of the original habitat which occurred within eThekwini Municipality still remaining (McLean C., 2016).

1.2 Justification

In 2012, conservation management staff from the Natural Resources Management Division of the Parks, Leisure and Cemeteries Department, eThekwini Municipality raised concerns regarding the increased presence of *Dalbergia obovata (D. obovata)* in the coastal grasslands. If *D. obovata* was establishing in grasslands it could, as an indigenous species be considered as an emerging bush encroachment species. For the purpose of this study, indigenous species bush encroachment is regarded as having the same outcome as invasion by invasive alien plants in that unless controlled, the end result is a transition to a near mono species bush or tree cover (Ansley et al., 2006, Archer, 2010) with a permanent loss of the grassland habitat and its associated indigenous herbaceous species.

1.3 Literature review

Dalbergia obovata is a member of the Fabaceae. *Dalberg*ia includes representative species in Africa, South America, southern and eastern Asia, the tropical Indo-Pacific, Madagascar and Australia. Relatively little is known about *D. obovata* as a species other than general information describing it as a climber which uses tendrils, its flowering and fruiting times, and taxonomic information. Unlike other economically important *Dalbergia* species such as *D. sisoo, D. melanoxylon* and *D. nigra*, no records were found describing the phenology of *D. obovata*. Various gardening websites and work done at the eThekwini Silverglen Nature Reserve medicinal plant nursery (Nichols, 2017) state that seeds should be removed from seed pods and scarified in order to germinate but no studies have been undertaken to determine how that would happen in the natural environment or how the seed dispersal takes place. Available literature (Coates-Palgrave, 1977, Pooley, I993), describe *D. obovata* as a liana or creeper which scrambles through forest canopies and which occurs in coastal and scarp forests and riverine forests along the Eastern coast of Southern Africa, in low altitude dune forest, swamp forest, coastal forest, scarp forest, riverine forest and valley thicket (Acocks, 1988, Thomas, 2004) and on the edges of forests on hill slopes. It is also recorded that it can occur as a tree which attains a maximum height of 6m both in the wild and as a cultivated shrub and occurs along the Eastern coastal areas of Sub Saharan Africa from the Eastern Cape to Northern Mozambique or Southern Tanzania from sea level to an approximate altitude of 900m. During this investigation it was established that *D. obavata* seeds are small kidney shaped beans averaging 6.5 mm in length and 0.0764 grams in mass. The seed pods are generally elongated, flattened and tapered at the base and apex with either a single seed contained at the approximate mid-point or a pair of seeds contained at the 1/3 and 2/3 position along the length of the seed pod. Single seed pods average 40mm in length and double seed pods average 57mm in length. The width of the pods is a fairly consistent 11mm (Chapter 3) and the general morphology of the seed pod conforms to that of a wind dispersed winged seed (Greene and Johnson, 1989). No separation of the seed pod and release of the seeds has been observed or recorded and for the purposes of this investigation it was assumed that the seeds of *D. obovata* are dispersed together with the pods and are therefore referred to as diaspores. In the absence of detailed information pertaining to *D. obovata* the general physiology, growth and development characteristics of lianas as a group are taken into consideration.

Bush encroachment into grasslands, by C3 woody plants is recognised as a worldwide phenomenon (Naito and Cairns, 2011). A full discussion and consideration of the various equilibrium, non-equilibrium and dis-equilibrium models (Gordijn and Ward, 2010), of bush encroachment is beyond the scope of this investigation and is limited to the concepts that are necessary to provide a backdrop against which the investigation of the encroachment of *Dalbergia obovata* into moist coastal grasslands can be discussed. The role of fire, MAP, competition between grasses and woody plants for resources and the contribution of herbivores is covered more extensively in chapter two. The global phenomenon of woody plant expansion into grasslands has been cited as evidence for increased atmospheric CO_2 levels as a global driver of bush encroachment (Wigley et al., 2009) and is supported by evidence available from the global analysis of tree rings which correlates to an increased growth rates of trees in response a global increase in atmospheric CO_2 (Myneni et al., 1997). Investigations into the phase transition of prairie to woodland has indicated that the threshold level at which encroachment becomes self propagating unless the underlying drivers of encroachment are removed is approximately 18% to 20% (Loehlel et al., 1996). C3 plant species normally associated with bush encroachment are either trees or shrubs. Typical examples being *Acacia* spp (Bond and Midgley, 2012), *Terminalia* spp, *Dichrostachys cinerea*, *Colophospermum mopane*, (De Klerk, 2004), mangroves (Saintilan and Rodgers, 2015), *Prosopis glandulosa* and *Juniperus* spp (Cabral et al., 2003, Afinowicz, 2004) and *Ulmus pumila* (Su et al., 2015). Literature searches have not identified any cases of bush encroachment by species of lianas.

In a parallel phenomenon to the global encroachment of grasslands by woody plants, forests globally have experienced a similar increase in the abundance of lianas (Laurence et al., 2001, Phillips et al., 2002, Gallagher and Leishman, 2012, Yorke et al., 2013). The increased growth rate of lianas in the presence of increased CO_2 (Zotz et al., 2006) has also been cited evidence of CO_2 as a global driver of liana expansion together with local habitat disturbances (Schnitzer and Bongers, 2011, Yorke et al., 2013). Results reported in literature for the estimation of liana population increase in forests vary depending on the methods used with no apparent standardisation of survey methods. Schnitzer and Bongers, (2011), observed a doubling in stem counts and basal stem area whereas Phillips et al.,

(2002) recorded an increase in canopy cover from 33% to 75% of the canopy area where previous studies on the distribution of lianas estimate that lianas comprise up to 33% of tropical forests. Assessments of liana distribution within tropical forests (Yorke et al., 2013) indicated there is a negative correlation between the frequency of liana stems and basal stem diameter in relation to distance from the edge of the forest, with a decrease in the number of plants in response to an increased distance from the edge (Laurence et al., 2001). Conversely the average basal stem diameter increased with distance from the edge of the forest. This was confirmed by Londré and Schnitzer, (2006) who concluded that there was a marked decrease in liana density towards the centre of forests. It is suggested that this spatial pattern of lianas within forests is in response to habitat fragmentation as opposed to elevated CO_2 or climate change and that lianas appear to benefit from habitat fragmentation and associated increases in forest edges (Londré and Schnitzer, 2006, Arroyo-Rodríhuez and Toledo-Aceves, 2009). Schnitzer and Bongers, (2011) cited four methods of propagation utilised by lianas to cover gaps in the forest canopy; (i) seed dispersal and germination, (ii) advanced regeneration of damaged stems, (iii) lateral growth of branches along the forest floor with rooting and generation of vertical growth and (iv) long distance clonal recruitment via vines in the canopy which fall to the ground and then root.

Although there are parallels between encroachment of woody plants into grasslands and the increase of lianas in forests there are also significant differences in that with the exception of *Toxicodendron diversifolia* in North America which can occur as shrubs of 3.8 – 4m high (Badel et al., 2015) and *Secamore sparsiflora* in Madagascar, (Lahaye et al., 2005), no references were found pertaining to liana species which had encroached into grassland habitats outside of forests.

The evolution of lianas has resulted in significant modifications in the mechanical and hydraulic characteristics of liana trunks (Lahaye et al., 2005). In self-supporting plants, the stems or trunks have to resist axial compression as a result of gravity and the crown weight (Badel et al., 2015) and a combination of stiffness and flexibility to resist lateral bending or breaking as a result of wind or loads due to the mass of ice, snow or fruit. Lianas or non-self-supporting climbers (Rowe and Speck, 2005, Gianoli, 2011) have a growth advantage over self-supporting plants in that they are able to achieve

vertical growth and large areas of leaf surface by using other plants for support without having to invest energy and biomass in the building of support trunks to support the weight of branches and leaves and resist dynamic loading (Rowe and Speck, 2005, Isnard and Silk, 2009). Lianas are therefore able to invest in supernumerary or secondary cambium tissue (Isnard and Silk, 2009) which allows for an increased hydraulic capacity in relation to stem diameter. Where the above ground portions of lianas may only be 5% of a forests biomass, the leaf area may actually comprise 33% of the canopy allowing for a high ratio of leaf weight and surface area to xylem. Yorke et al., (2013), reported that the branches of large lianas can extend in a radius of up to 500m from their main stem or trunk. The reduced carbon investment and nutrient requirements required for the growth of flexible stems combined with the increased hydraulic capacity per unit measure of stem diametre and increased leaf area to biomass ratio therefore gives lianas a competitive advantage over self-supporting trees in forests (Schnitzer and Bongers, 2011).

Analysis of the genome size in regard to the evolution of *Dalbergia* (Hiremath and Nagasampige, 2004) found that climbing members of the genus have a significantly higher genome content indicating that *Dalbergia* climbers evolved from tree like forms via a process of acquiring extra genes. Investigation into the developmental growth patterns of *Secamore sparsiflora* (Lehaye et al., 2005) suggests that it achieves a shrub like form via the addition of genes to partially suppress the transition from stiff juvenile stems to compliant and flexible adult stems with the growth of anomalous cambium tissue. The self-supporting phase observed in climbers such as *Toxicodendron diversifolia* and *Bauhinia guyanensis* (Rowe and Speck, 2005) is limited to the juvenile phase of growth which may be extended until the plant comes into contact with a host and that the evolution of the climbing growth form may limit reversion to a fully self-supporting growth form. The implication is that unless lianas are able to attach to a host plant and complete their development, they remain in a state of immaturity.

1.4 Key research questions

Three key questions were identified regarding the encroachment of grasslands by *D. obovata*.

1.4.1 Is there substantive evidence that *D. obovata* is actually encroaching into the grasslands or are changes in its distribution attributed to changes in forest boundaries and woody vegetation cover

as a result of reserve management practices?

1.4.2 What are the wind dispersal patterns of *D. obovata* diaspores and is there a critical position that the parent plant must occupy on the host trees canopy in order for diaspores to escape the forest's boundary?

1.4.3 How does *D. obovata* grow and propagate once it becomes established in the grassland?

A subsequent question that was raised as a result of field surveys of *D. obovata* distribution in the grasslands, was the identification and mapping of large dense stands of *D. obovata* which appeared to show no evidence of canopy contact mortality and excluded all other plant species within the area covered by the stands canopy. If this was the case then how was *D. obovata* able to avoid the $^{-2}/_{3}$ Power Rule of self thinning?

1.5 Predictions

It was predicted that the encroachment of *D. obovata* into the moist coast grasslands would not be ascribed to a single factor or driver but that it will be shown to be a combination of global drivers and local factors such as the growth and development characteristics of climbers which provide lianas a competitive advantages within forests, seed dispersal characteristics, global drivers of bush encroachments and local factors such as habitat fragmentation, veld management practices and fire regimes.

1.6 Aims and objectives of Chapter 2 and Chapter 3

The aim of chapter two was to undertake an analysis of the available management records of seventeen nature reserves and conservation areas within the eThekwini Municipal boundaries in conjunction with field surveys and mapping exercises of the distribution of *D. obovata* undertaken in four of the management areas. The objective of these was the confirmation of whether or not D. obovata had encroached into the coastal grasslands. In Chapter three, the overall aim was to investigate the methods of the dispersal of diaspores beyond the edge of forests and the patterns vegetative propagation or reproduction of *D. obovata* once etsablished in the grasslands. Two objectives were identified for chapter three. In the first, a simplistic theoretical wind dispersal model

was developed in order to test the relationship between the positioning of *D. obovata* in the canopy of host trees and the successful dispersal of diaspores beyond the forest's edge. The second objective was to map the exact positions of individual plants within established stands in the grasslands and their interconnecting root systems in order to determine the rates at which the stands expanded over time and confirmation of clonal propagation as a method of vegetative reproduction by *D. obovata*.

The final discussions of the results from chapters two and three are considered in the context of the physiology and other attributes of lianas together with the possible effects of global drivers of encroachment presented in chapter one.

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CHAPTER 2: **An investigation of the encroachment of sub-tropical moist coast grasslands within the urban nature reserves of Ethekwini Municipality by *Dalbergia obovata*, an indigenous forest liana**

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2.1 Abstract

The encroachment of a forest liana, *Dalbergia obovata*, into moist coast grasslands within urban nature reserves in eThekwini Municipality was identified as a concern by reserve management . Any encroachment by woody plants has the potential to reduce the viability of the remaining patches of this threatened habitat with a resulting loss of biodiversity. *D. obovata* has not previously been recorded as an encroacher species in grasslands. An analysis of the available management records and status of *D. obovata* in seventeen urban nature reserves and conservation areas was undertaken. A field survey of the general distribution patterns of *D. obovata* was also undertaken to verify the accuracy of the analysis of the management records and the results were captured as layers on a Geographic Information System (GIS). The results of the Chi-square test and Principal Components Analysis together with the final GIS based maps confirmed that in the absence of large herbivores *D. obovata* was not effectively controlled through historic bush encroachment management practices. *D. obovata* could no longer be considered as occurring in only forest or woodland habitats but has successfully encroached into the moist coast grasslands of the reserves of eThekwini Municipality and represents a further threat to this already threatened grassland habitat.

12.2 Introduction

The City of Durban (eThekwini Municipality) is situated within the Maputuland – Pondoland – Albany biome biodiversity hotspot (Boon et al., 2016). According to McLean, (2016), 2267 indigenous plant species or approximately nine percent of the total indigenous plant species list for South Africa have been recorded within the cities boundaries. A significant percentage of these plants occur within the remaining grasslands. These grasslands largely comprise Kwazulu-Natal Sandstone Sourveld which is separated into two sub types by an escarpment at approximately 400m – 450m (Boon, 2017). Thus there is a drier inland region which is more typical of KZN Sandstone Sourveld and a coastal belt with a higher mean annual precipitation (MAP) of 819 mm to 1272 mm (Mucina et al., 2006) which falls into the category of wet, moist or mesic grasslands (Devine et al., 2017). These mesic grasslands tend to be unstable in composition (Sankaran et al., 2005) and comprise complexes of grass and woody species the proportions of which are influenced by local conditions such as the frequency and intensity of fires (Govender et al., 2006, Joubert et al., 2012, Devine et al., 2017). Moist coast grassland are also listed as the most threatened of the South African grassland ecosystems (Cadman et al., 2013). Less than 8% of the original grasslands which occurred within eThekwini Municipality are left (McLean, 2016). A number of threats to these remaining grasslands have been identified and include invasion by invasive alien plant species (IAPs) (Richardson and van Wilgen, 2004), change in land use from undeveloped open space to developed transformed land (Rouget et al., 2016), land invasion by informal settlements (Pithouse, 2016) and bush encroachment (Cadman et al., 2013).

For the purpose of grassland management the uncontrolled encroachment of grasslands by indigenous woody species is regarded as having the same outcome as invasion by IAPs in that unless encroachment is controlled, the end result is a transition to a near monospecific vegetation cover with permanent loss of the grassland habitat and its associated indigenous herbaceous species (Ansley et al., 2006). In 2012 *D. obovata* was identified by managers of nature reserves within eThekwini Municipality as having an increased abundance within the coastal grasslands. Encroachment by *D. obovata* into grasslands within the city or Kwazulu Natal was not found in any of the available literature or management records.

Bush encroachment, is recognised as a worldwide phenomenon (Naito and Cairns, 2011). 'Walters Two Layer model' (Walter and Mueller-Dombois, 1971) provided a model of tree - grass relationships in dry savanna based on the principle of 'vertical niche separation'. In this model the rooting depth of adult trees and grasses is identified as occurring in two distinct layers. Since grass species tend to have shallower but denser root systems they are able to efficiently exploit available upper soil water from limited rainfall. Conversely, adult trees have deeper roots and are able to access the deeper ground water. However tree seedlings with their shallower root systems have to compete directly with the grasses for available water in the upper soil layer. Vertical niche separation has been used to identify overgrazing as a driver of bush encroachment in dry savanna and rangelands (Ansley et al., 2006 , Ward, 2010) where removal of grass cover results in greater availability of water for tree seedlings that are then recruited into the adult population. In grasslands that receive more than 650 mm MAP, water is more readily available and is not a factor limiting maximum tree coverage (Devine et al., 2017) and the limiting resources are nutrients and light (Riginos., 2009, Moustakas et al., 2013). In grasslands with an annual rainfall exceeding 650mm MAP threshold, suppression of bush encroachment is related to the fire returns frequency, fire intensity and the susceptibility of tree seedlings to grassland fires (Higgins et al., 2000, Bock et al., 2007). This, in conjunction with competition from grasses for resources, prevents recruitment of the seedlings into the population of adult trees.

State and transition models (Stringham et al., 2003, Meyer et al., 2007, Johanson, 2011), provide a working platform for the interpretation of tree – grass dynamics and bush encroachment in moist or humid grasslands where the proportional influence of global drivers such as increased atmospheric CO_2 or temperature, and/or local factors such grazing intensity in combination with competition for resources such as water and nutrients, the impact of fire regimes or shifts in annual rainfall may cause the shift of an ecosystem from one state to another. These potential changes in ecosystem states may include shifts from grasslands to savanna, from savanna to forest or the converse. State and transition models also assume that since there is a dynamic response of habitats to environmental conditions there is an implication that bush encroachment is a naturally 'self' reversible condition if the drivers of

encroachment are removed and local factors are manipulated by land management practices. Reversal of encroachment does not however automatically restore the herbaceous species that were lost as a result of bush encroachment (Ansley et al., 2006), especially if the bush encroachment coincides with habitat fragmentation and IAP invasion (Archer and Predick, 2014).

The global phenomenon of woody plant expansion into grasslands has been cited as evidence for a global driver of bush encroachment (Wigley et al., 2009). Further evidence in support of CO_2 as a global driver of bush encroachment has been provided by the analysis of tree rings which have shown a correlation between increased growth rates of trees and the global increase in atmospheric CO_2 (Battipaglia et al., 2013). C3 trees growing under conditions of elevated CO_2 are therefore able to increase the allocation of carbon storage to their roots (Curtis and Wang, 1998) which allows for an increased availability of stored resources for the regeneration of photosynthetic capacity after fires, an increased post burn recovery rate (Bond and Midgley, 2012) and an increased recruitment of tree seedlings into the adult population. Studies undertaken in Ithala Game Reserve (Gordijn and Ward, 2010) and the Hluhluwe-iMfolozi Game Reserve (Case and Staver, 2017) have also shown that veld fires conducted at historic frequencies as per the nature reserve's veld management programs, are no longer controlling bush encroachment.

Dalbergia obovata is described as a liana in the Fabaceae family which occurs along the eastern coastal areas of sub-Saharan Africa from the eastern Cape to northern Mozambique and southern Tanzania from sea level to an approximate altitude of 900m. It has been recorded in several forest habitats including dune forest, swamp forest, coastal forest, scarp forest, riverine forest and valley thicket (Coates Palgrave, 1977, Pooley, 1993) and on the edges of forests on hill slopes where it may occur as a tree or shrub up to 6m in height. There is however no mention by any authors of the plant being considered as a grassland species and relatively little is known about *D. obovata* as a species other than general information describing it as a climber which uses tendrils, its flowering and fruiting times, and taxonomic information. The species is described as flowering from October to November and that the mature winged flattened seed pods ripen from February to March.

In a parallel phenomenon to the global encroachment of grasslands by woody plants, forests globally are experiencing a similar increase in the abundance of lianas (Schnitzer and Bongers, 2011., Yorke et al., 2013). However, with the exception of a limited number of examples, such as *Toxicodendron diversifolia* in North America which can occur as shrubs of 3.8 – 4m high and *Secamone sparsiflora* in Madagascar (Lahaye et al., 2005), there is very little references in literature to liana species that occur outside of a forest habitat.

The question that therefore needs to be answered is whether or not *D. obovata* is actually actively encroaching into the grasslands. On the assumption that, because *D. obovata* is a forest liana, it's distribution is determined by changes in forest boundaries, it was hypothesised that *D. obovata* in grasslands was a passive result of management practises aimed at controlling encroachment by other woody species e.g., grassland burning and mechanical and chemical bush control. In order to confirm this a twofold approach was taken. The first step was an analysis of the reserve management records from seventeen nature reserves and conservation areas within the Ethekwini Municipality. The results of this were then 'ground truthed' by selecting four nature reserves for field surveys.

2.3 Methods

2.3.1 Analysis of Management practices and records of *D. obovata* encroachment

From the available Durban Metropolitan Open Space Systems (D'MOSS) layer of Ethekwini Municipal Geographic Information Systems (GIS) database, ten nature reserves and seven conservation areas containing either moist coast grasslands or KZN Sandstone sourveld were selected between an altitude of 50m above sea level and 600m above sea level. One nature reserve was divided into four management areas on the basis of each area being distinctly separated from the other areas and having different management programs. This then provided a total of twenty study areas (Appendix 1).

The management records for each study area were obtained and data extracted regarding the historic frequency of veld fires, whether or not the fires were planned or unplanned, the season in which burns occurred, the intensity of fires as indicated by the use of head fires versus back fires, the use of fire-

breaks around forest margins as opposed to allowing fires to burn into the forest margins, the presence of IAPs and IAP clearing programs, woody plant encroachment into the grasslands and implementation of bush encroachment control programs, the presence of large herbivores, (either bulk grazers or mixed feeders) and whether or not encroachment into the grasslands by *D. obovata* had been recorded by the reserve managers.

The summarised results of the extracted data were captured in an XL table with management components entered as the independent variables and recorded encroachment by *D. obovata* as the dependant variable. Recorded encroachment was assigned score of 1 and an absence of D. obovata was recorded as 0. Scores were as nominal values or categorical data. The strength of the relationship between management practices and *D. obovata* encroachment was analysed by performing a Pearsons Chi- Square test and a Principal Components Analysis. The Chi-square and PCA tests were run with management variables entered as fourteen individual components. For the PCA test only the coefficient scores pertaining to the correlation between the management components and encroachment by *D. obovata* as the dependent variable were considered as this was the relationship being tested for.

2.3.2 Field surveys of *D. obovata* distribution and mapping of individual stands of *D. obovata*

From the results of the management practices versus *D. obovata* encroachment analysis, three reserves and one conservation area were chosen for a ground level survey of *D. obovata* distribution patterns. The field survey area were selected on the basis of being below the altitude of 350m which placed them well below the transition zone of coastal grasslands to KZN sandstone sourveld and that they also had well documented management histories. This was done in conjunction with the analysis of the available orthophotos of the survey areas which were provided by the Ethekwini Land Survey department for the years 1999 to 2016. Since *D. obovata* is deciduous the lack of foliage during the dry season prevents accurate identification of the plant amongst other vegetation. Surveys were therefore restricted to the growing season from September to late February when flowering and production of seed pods also occurred. This aided the identification of *D. obovata* plants in the forest canopies. Due to the absence of previous surveys of *D. obovata* there was no existing data base

against which comparisons of previous mapping exercises of the spread and densities could be made. Conventional methods used to estimate the infestation rate of IAPs or encroachment of woody plants rely on the ratio of stem counts per sample area, percentage canopy cover of the sample area and the height of plants using representative numbers of quadrats or line transects which are then extrapolated to the entire survey area (Elzinga et al., 1998). The use of percentage canopy cover is useful for large moribund stands of plants but lacks accuracy when estimating the density of seedlings or the number of plant stems and the use of stem counts requires the removal of the canopy cover which becomes labour intensive. A minimum representative sampling of five percent of the grassland cover visible in the 1999 orthophotos, using five random 100m^2 quadrats per hectare for a total of 190.43ha of grassland to be surveyed across four nature reserves would have required 950 quadrats. The estimated time required to undertake this was calculated at 2190 hours and made conventional sampling using quadrats or line transects infeasible for this survey.

Remote surveys based on the analysis of aerial photos and satellite images have been used successfully to survey large areas with the use of quadrats or transect sampling to confirm the accuracy of the remote survey results thereby reducing the time and labour component required for conventional surveys (Kotzé et al., 2010). It has however been noted that high resolution aerial photos of less than 10m resolution are required for accurate identification of trees and shrubs (Forsyth, 2012). The rambling growth form of *D. obovata* results in branches growing through the canopies of other vegetation as well as the similarity of the plant to other indigenous grassland woody species in its early growth stages was considered as a confounding factor in remote sensing. This was exacerbated by a lack in consistency in the time of year in which the aerial surveys from which the aerial photos used in this study were flown by the Ethekwini survey department. Since *D. obovata* loses its leaves during the dry season it cannot be detected among other vegetation using analysis of aerial photos taken during the winter. The common approach noted in available literature in bush encroachment and IAP infestation surveys was to either record the presence or absence of IAPs or woody encroachers, or to focus on the degree of infestation based on stem or canopy cover ratios to the surface area of the land being surveyed. No literature was found which set a threshold value based on which an areas was considered encroached or not encroached. The assessment method used for the annual field

assessment and management of IAPs within the Ethekweni Municipal Nature Reserves was therefore adopted and applied. In this method simplified categories of woody plant to grass ratios were used aid with the visual assessment of large areas of vegetation. These categories were 1:1m^2 – 1:4m^2, 1:4m^2 – 41:16m^2, 1:16m^2 – 1:64m^2, 1:64m^2 – 1:400m^2, 1:400m^2m2 – 1:2500m^2 and less than 1:2500m^2 and where a ratio of IAP's to indigenous vegetation of 1:64m^2 was considered to be invaded. The estimation of *D. obovata* densities was therefore based on the ratio of *D. obovata* plants to a given area of grassland or a visible portion of *D. obovata* per area of forest canopy and a ratio greater than 1:64m^2 or 6.5% was considered to be encroached. Prior to the commencement of the field survey the method was calibrated by setting up a series of 4m x4m test plots along a transect in Marian Wood nature Reserve starting from the edge of the forest and running 100m into the grassland over an area encroached by *D. obovata*. This permitted the use of a laser range finder and maps overlaid with a ten metre by ten metre grid to estimate the distribution of *D. obovata* plants. The results were captured as layers on a GIS project which allowed comparison of changes in the grassland and woody vegetation cover from 1999 to 2015 against the occurrence of *D. obovata* recorded during the survey.

2.4 Results

2.4.1 Results of the analysis of Reserve Management practices and recorded *D. obovata* encroachment

Mixed results were obtained from the records of *D. obovata* encroachment and reserve management practices with ten of the management areas or 45% of the grasslands recorded as having been encroached by *D. obovata* and eleven of the management areas or 55% as having no encroachment (Appendix 2). The Pearson's Chi Square tests (Appendix 3) indicated a significant association ($P<0.05$) between the absence of large mammalian herbivores in the grasslands and *D. obovata* encroachment. There were no significant associations between *D. obovata* encroachment and other management practices, such as the season, frequency and intensity of fires, the occurrence of encroachment by other woody species, or the control of IAPs ($P>0.05$).

The results obtained from the PCA identified four axis which accounted for 82.29% of the total variance (Appendix 4). The first axis (Appendix 4), accounted for 39.46% of the variance, the second

for 17.07% , the third was 16.42% and the fourth axis accounted for 9.33% of the variance. The scores obtained from the correlation matrix (Appendix 5) gave a correlation of -0.522 for both bulk grazers and mixed feeders, -0.369 for head fires and 0.369 for back fires. Only the correlation of management variables to encroachment by *D. obovata* (Appendix 5), were considered as this was the relationship being tested for. Other correlation scores between the management variables were therefore disregarded. The remaining components had correlations lower than 0.30. This indicated that bulk grazers and mixed feeders (large herbivores) accounted for the greatest proportion of the variance and was best correlated to the first two principle components identified by the eigenvalues.

2.4.2 Results of the distribution mapping of *D. obovata* within four survey sites

The mapped distributions of *D. obovata* within the four selected survey sites at New Germany Nature Reserve, Roosefontein Nature Reserve, Palmiet Nature Reserve and the UKZN Westville Campus are presented in Appendices. 7 to10 and show that *D. obovata* was not uniformly distributed but occurred in patterns of densities ranging from a maximum density of 1:1m^2 to a minimum of ≥1:2500m^2. The extent of the grassland area which had been encroached by *D. obovata* when compared against the 1999 orthophotos is presented in Appendix 6.

In New Germany Nature Reserve the four management blocks (Appendix 7) had different levels and patterns of encroachment. Approximately 4724m^2 or 5.2% of the available grasslands in Block 1 had been encroached by *D. obovata* where it occurred in bands of short stunted plants within the fire breaks on the boundary of forests and along road verges with some isolated stands within the grasslands. In Block 2, *D. obovata* was restricted to the edges of the bush clumps. In the combined management blocks of 4&5, the grassland loss to bush encroachment was calculated at 3381m^2 or 2.81 % with no observed encroachment of *D. obovata.* Blocks 4&5 were identified from the reserve management records as being one of the areas that had mixed feeders, all of which had no *D. obovata* encroachment. Block 3 was recorded as the only management area where programs of brush clearing and controlled burns have resulted in a significant increase in grassland cover of 35644m^2 or 91%. However a total of 58119m^2 or 76.53% of the grassland in Block 3 was encroached by *D. obovata.*

The total *D. obovata* distribution patterns for Roosefontein Nature Reserve (Appendix. 8) records that 193034m^2 or approximately 8% of the reserve has very high *D. obovata* densities of 1:1m^2 – 1:4m^2 which were located either along the edges of roads or on the North East facing slopes on the western boundary of Merrivale North and Merrivale South management blocks. Appendices 11 – 14 provide photographic examples of these distribution patterns within the reserves. Of particular note was a stand in the main Roosefontein block (Appendix 14), of approximately 20011m^2 in extent which is almost 100% *D. obovata.* A further 1090164m^2 or 45% of the combined reserve area has *D. obovata* densities of 1:4m^2 – 1:64m^2. A further 576171m^2 or 24% of the reserve has *D. obovata* densities of 1:64m^2 – 1:400m^2 which are restricted to areas of forest. The remaining 540370m^2 or 22.52% of the reserve comprises grasslands with *D. obovata* densities of less than1:400m2 – 1:2500m^2.

The vegetation of Palmiet Nature Reserve is 98.9% scarp forest and riverine forest with two small fragmented grasslands on the Dawncrest and Faurea ridges amounting to a total of 2754m^2 . The combined grassland cover showed a net increase of 7.5%. Patches of medium to high density stands of *D. obovata* were recorded on the borders of the grasslands and between groups of trees on the fringes of the forest (Appendix 9) and which displayed the same growth patterns as the plants observed within the fire break areas of New Germany Nature Reserve.

The UKZN Westville campus had the highest rate of grassland loss to bush encroachment and IAPs (Appendix 10). Of the original 362827m^2 of grassland visible on the 1999 orthophotos only 204069m^2 or 56.24% remained at the time of the survey representing a 63.27% loss over an eight year period through a combination of bush encroachment, development of road infrastructure and land invasion by the adjacent informal settlement. The recorded patterns of *D. obovata* encroachment in the original grassland areas and remaining eastern grasslands were similar to those observed in the other three nature reserves. Where all of the M19 hillside grasslands have been lost through bush encroachment and IAP invasion, medium to high levels of *D. obovata* encroachment of approximately 1:16m^2 – 1:400m^2 were recorded. Approximately 43% of the eastern grassland area had medium to high density *D. obovata* encroachments of 1:4m2 – 1:64m^2 which occurred along the edges of the grasslands

adjacent to roads, the bottom of watercourses and areas which were previously grassland. Less than 60% of the area was estimated to have a medium to low density of 1:64m2 – 1:2500m^2. The highest levels of *D. obovata* encroachment of 1:1m^2 – 1:4m^2 and were restricted to a narrow band alongside the road verges and parking lots adjacent to the Palmiet Valley.

2.5 Discussion

The results of the analysis of the management records and ground level surveys were unexpected since *D. obovata* is a forest liana and the assumption was that its distribution would be determined by the contraction or expansion of it's preferred forest habitat. Expansion of *D. obovata* into grasslands was therefore expected to coincide with certain management practices aimed at controlling bush encroachment.

The Chi-square and PCA test results only indicate the strength of associations and relationships between components and variables but don't explain causality. With regard to the influence of fire frequency, fire season, and fire intensity the available literature indicates that an increase in fire frequency should suppress bush encroachment (Sankaran et al., 2008, Gordijn and Ward, 2010, Case and Staver, 2017). Therefore if changes in *D. obovata* distribution are in response to changes in forest and woodland cover then increased fire frequency should be associated with a corresponding decrease in *D. obovata* distribution as would burning in late winter of early spring, and the use of head fires (Govender et al., 2006, Bock et al., 2007). However in the management area block No.3 of New Germany Nature Reserve (Appendix 7), significant encroachment by *D. obovata* has occurred despite an increase in grassland cover and a decrease in bush encroachment by other woody species. From the summary of reserve management practices (Appendix 2) it was noted that this reduction of general woody encroachment was achieved in conjunction with the application of fire management programs where head fires were used in early spring and allowed to burn into the bush clumps. This indicated that woody encroachment by species other than D. obovata can be achieved through correctly planned burning programs (Higgins et al., 2000, Bock et al., 2007) . By contrast the low correlation matrix scores obtained from the PCA tests (Appendix 5) for the use of head fires, back burns and and

frequency of fires, AIP and bush encroachment control and the use of fire-breaks indicated very weak correlations between conventional bush encroachment management practices and the prevention of encroachment by *D. obovata*. The weak positive correlation associated with the use of head fires may however explain the pattern of short stunted *D. obovata* plants observed on the borders of forests and within fire-breaks where controlled burning is implemented. Although the fire does not prevent the spread of *D. obovata*, it may keep them trapped within the top kill zone as Gullivers (Higgins et al., 2000). Conversely, the correlation matrix recorded a negative correlation between the presence of large herbivores in the grasslands and encroachment by *D. obovata*. The PCA results thus confirm the Chi-square results which found no relationship between any of the management practices but established that there is a relationship between the absence of bulk grazers and mixed feeders and encroachment of the grasslands by *D. obovata*.

It is generally accepted that mixed feeders and grazers are associated with the removal of grasses which compete with woody plants for nutrients and light (D'Onofrio et al., 2015) thereby allowing woody plant seedlings to establish themselves more successfully. However the reserve management records (Appendix 2), show that in all instances where mixed feeders and bulk grazers were present in a reserve or a management block of a reserve no encroachment of *D. obovata* into that particular grassland had occurred. This was supported by the field surveys (Appendixes 6 to 10) where no encroachment by *D. obovata* was recorded in blocks 4&5 at New Germany Nature Reserve where mixed feeder herbivores were present. Similar patterns of suppression of woody encroachment by large herbivores have been recorded in Australia (Maher et al., 2010), Northern China (Su et al., 2015) and East Africa (Sankaran et al., 2013) where exclusion of large herbivores resulted in the subsequent increased encroachment of grasslands by woody plants. Investigation of the role of large herbivores in "Rewilding" projects in the Netherlands (Cornelissen et al., 2014) demonstrated that bulk grazers and mixed feeders can reduce bush encroachment by specific plant species such as *Sambucus nigra* and *Salix* spp and promotethe establishment of grasses and other herbaceous species. Cattle and horses have similar dietary patterns to wildebeest, and zebra whereas deer species have similar diets to impala and free ranging domestic goats (Gebert and Verheyden-Tixier, 2001, Dunham, 1982, Raats, 1998). Thus, although overgrazing by large herbivores is normally associated with bush encroachment

it may be also be effective in the reduction of specific woody species in grasslands.

In the ground level surveys *D. obovata* was recorded as being present in all of the grasslands surveyed where large herbivores were absent (Appendixes 6 to 10) and tended to occur in distinct patterns of high density bands on the edges of forests and bush clumps and decreased with increasing distance from the forest-grassland boundaries towards the centre of the grasslands where small isolated stands and low density scatterings of plants in grasslands occurred. Although the mechanisms and patterns of propagation and diaspores dispersal of *D. obovata* did not form part of this investigation, the pattern of decreasing plant densities relative to the forest borders indicates that encroachment into the grasslands by *D. obovata* is a progressive linear process. The dense stands of 100% *D. obovata* covering several hectares in extent (Appendixes 9 and 14) and smaller stands of *D. obovata* recorded in the grasslands of the survey areas (Appendix 14) indicate that encroachment by *D. obovata* results in the complete exclusion of other indigenous species. This does not conform to bush encroachment where an ecosystem shift occurs from grassland habitat to woodland or forest habitat (Stringham et al.,2003, Johanson, 2011) but is more analogous with mono species IAP invasions (Ansley et al., 2006, Archer, 2010) with a corresponding loss of biodiversity. Although the threshold level for classifying an area as encroached was set at a ratio ≥1:64m^2, *D. obovata* plants were recorded as being established at lower densities in all of the study areas except for management blocks 4&5 at New Germany Nature Reserve and the implication being that encroachment had already started wherever large herbivores were absent.

2.6 Conclusion

In consideration of the presentation of evidence in available literature for the influence of global drivers such as increased CO_2 and mean annual temperature which have resulted in the increased growth rates of woody plants and liana species in particular and in the absence of any previous literature citing forest liana species as encroaching into grasslands it was expected that the expansion or contraction of *D. obovata* populations in moist coast grasslands would correlate with general bush encroachment. It was also expected that any expansion of *D. obovata* within the grasslands would

therefore be a result of management practices which promote or suppress bush encroachment. The results of the analysis of management practices compared to encroachment by *D. obovata* and the results of the field surveys have shown that traditional bush encroachment management practises based on historical grassland burning regimes have not prevented the encroachment of *D. obovata* into the moist coast grasslands within the study areas. The results of the ground level surveys have also shown that the historical assumption that *D. obovata* is restricted to forests and woodland habitats is no longer correct and that *D. obovata* has successfully encroached into the grasslands outside of the forest habitat. A relationship between the absence of large herbivores in the grasslands of the study areas and the encroachment of *D. obovata* in moist coast grasslands was also identified although the mechanisms are not currently understood. It is therefore concluded that in the absence of large herbivores, *D. obovata* has become a bush encroachment species within the moist coast grasslands with the capacity to permanently transform this threatened habitat into mono species stands with a corresponding loss of biodiversity.

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12.9 Appendices to chapter 2

Appendix 1. Reserve/conservation management areas identified from the eThekwini GIS data base for surveys of *D. obovata* encroachment vs management practices.

Area number	Reserve / Conservation area	GPS coordinates	Altitude	Property ownership
1	Treasure Beach Grasslands	29° 56' 39.25" S 30° 59' 53.00" E	90m	Ethekwini Municipality
2	Kenneth Stainbank Nature Reserve	29° 54' 33.75" S 30° 56' 13.45" E	150m	Ezemvelo KZN Wildlife
3	Silverglen Nature Reserve	29° 56' 00.00" S 30° 52' 53.85" E	50m – 210m	Ethekwini Municipality
4	Roosefontein Nature Reserve	29° 51' 41.20" S 30° 55' 28.85" E	80m – 190m	Ethekwini Municipality
5	UKZN – Westville Campus	29° 49' 01.20" S 30° 57' 07.00" E	50m – 180m	University of Kwazulu Natal
6	Palmiet Nature Reserve	29° 49' 18.50" S 30° 55' 56.20" E	120m – 198m	Ethekwini Municipality
7	Nazareth Nature Reserve	29° 50' 47.20" S 30° 51' 49.50" E	185 – 315m	Ethekwini Municipality
8	New Germany Nature Reserve Block 1	29° 49' 00.77" S 30° 53' 14.50" E	280m - 390m	Ethekwini Municipality
9	New Germany Nature Reserve Block 2	29° 48' 46.10" S 30° 53' 20.30" E	330m - 380m	Ethekwini Municipality
10	New Germany Nature Reserve Block 3	29° 48' 36.64" S 30° 53' 51.12" E	310m - 350m	Ethekwini Municipality
11	New Germany Nature Reserve Block 4&5	29° 48' 29.17" S 30° 53' 30.50" E	250m - 340m	Ethekwini Municipality
12	kwadabeka Conservation Area	29° 45' 50.60" S 30° 53' 37.95" E	50m – 330m	Ethekwini Municipality
13	Trenance Park Nature Reserve	29° 39' 42.00" S 30° 00' 15.85" E	170m – 231m	Ethekwini Municipality
14	Marian Wood Nature Reserve	29° 50' 18.50" S 30° 50' 29.20" E	270m – 330m	Ethekwini Municipality
15	Inkonka Trust	29° 48' 39.60" S 30° 49' 05.70" E	450m – 530m	Ethekwini Municipality
16	Motala Heights conservation area	29° 48' 15.00" S 30° 49' 54.10" E	390m – 510m	Ethekwini Municipality
17	Edgecliffe Conservation area	29° 48' 08.95" S 30° 50' 34.55" E	401m – 511m	Ethekwini Municipality
18	Krantzkloof Nature Reserve	29° 46' 22.20" S 30° 49' 47.55" E	440m – 525m	Ezemvelo KZN Wildlife
19	Giba Gorge Nature Reserve	29° 48' 38.10" S 30° 46' 24.50" E	475m – 610m	Ethekwini Municipality / Private Partnership
20	Springside Nature Reserve	29° 46' 48.10" S 30° 46' 19.50" E	650m	Ethekwini Municipality

Appendix 2. Summary of the results of encroachment by D. obovata compared to management practices obtained from the available management records in the format required for the Chi-square and PCA tests.

Reserve / Conservation area	Management unit	EN	FF(a)	FF(b)	FS(a)	FS(w)	FS(s)	FI(hf)	FI(bf)	FB	IAPC	BEC	BG	MF
Treasure Beach Grassland Reserve	1	1	0	1	0	1	0	0	1	1	1	0	0	0
Kenneth Stainbank Nature Reserve	2	0	0	1	0	1	0	1	0	1	1	1	1	1
Silverglen Nature Reserve	3	1	1	0	1	0	0	1	0	1	0	1	0	0
Roosefontein Nature Reserve	4	1	1	0	1	0	0	1	0	0	1	1	0	0
UKZN - Westville Campus	5	1	1	0	1	0	0	1	0	0	1	1	0	0
Palmiet Nature Reserve	6	1	1	0	0	0	1	1	0	0	1	0	0	0
Nazareth Nature Reserve	7	0	1	0	1	0	0	1	0	0	0	1	1	1
New Germany Nature Reserve block 1	8	1	0	1	0	0	1	0	1	1	1	0	0	0
New Germany Nature Reserve block 2	9	0	0	1	0	0	1	1	0	0	1	0	0	0
New Germany Nature Reserve block 3	10	1	0	1	0	0	1	1	0	0	1	0	0	0
New Germany Nature Reserve block 4 & 5	11	0	1	0	1	0	0	1	0	0	0	0	0	1
Kwadabeka Conservation Area	12	0	1	0	1	0	0	1	0	0	0	1	1	1
Trenance Park Conservation Area	13	0	1	0	1	0	0	1	0	0	0	1	1	1
Marian Wood Nature Reserve	14	1	1	0	0	0	1	1	0	1	1	1	0	0
Inkonka Trust Conservation area	15	0	0	1	0	0	1	1	0	1	1	0	0	0
Motala Heights Conservation area	16	1	1	0	0	1	0	1	0	0	1	0	0	0
Edgecliff Trust Conservation area	17	0	1	0	0	0	1	1	0	1	1	0	0	0
Krantzkloof Nature Reserve	18	0	0	1	0	0	1	1	0	0	1	0	1	0
Giba Gorge Conservation area	19	0	0	1	0	1	0	1	0	0	1	0	0	0
Springside Nature Reserve	20	0	0	0	0	0	1	1	0	0	1	0	0	0

Key to abbreviations used in the table where
0 = No encroachment recorded,
1 = encroachment recorded

EN = encroached by *D. obovata*
FF(a) = Fire frequency annual
FF(b) = Fire frequency biannual
FS(a) = Fire season autumn
FS(w) = Fire season winter
FS(s) = Fire season spring
FI(hf) = Fire intensity - head fires
FI(bf) = Fire intensity - back fires
FB = Fire breaks maintained around forest
IAPC = Invasive Alien Plant Control programs
BEC = Bush encroachment control programs
BG = Bulk Grazers present
MF = Mixed Feeders present

Appendix 3. Summary of the Chi-square test results for the comparison of recorded encroachment of *D. obovata* in moist coastal grasslands against fourteen reserve management practises/components with acceptance or rejection of the null hypothesis.

Component	Null Hypothesis (Ho) and alternative Hypothesis (Ha)	Alpha	Chi Square	p value	Accept / reject Ho
EN / FF(a) (annual burn)	Ho = There is no association between the encroachment by D obovata in grasslands and annual burns. Ha = There is an association between the encroachment by D obovata in grasslands and annual burns.	0.05	0.900	0.343	Accept Ho
EN / FF(b) (biannual burns)	Ho = There is no association between the encroachment by D obovata in grasslands and biannual burns. Ha = There is an association between the encroachment by D obovata in grasslands and biannual burns.	0.05	0.900	0.343	Accept Ho
EN / FS(a) (autumn fires)	Ho = There is no association between the encroachment by D obovata in grasslands and the autumn fires Ha = There is an association between the encroachment by D obovata in grasslands and the autumn fires	0.05	0.020	0.888	Accept Ho
EN / FS(w) (winter fires)	Ho = There is no association between the encroachment by D obovata in grasslands and the winter fires Ha = There is an association between the encroachment by D obovata in grasslands and the winter fires	0.05	0.051	0.822	Accept Ho
EN / FS(s) (spring fires)	Ho = There is no association between the encroachment by D obovata in grasslands and the spring fires Ha = There is an association between the encroachment by D obovata in grasslands and the spring fires	0.05	0.002	0.964	Accept Ho
EN / FI(hf) (head fires)	Ho = There is no association between the encroachment by D obovata in grasslands and head fires. Ha = There is an association between the encroachment by D obovata in grasslands and head fires	0.05	2.716	0.099	Accept Ho
EN / FI(bf) (back fires)	Ho = There is no association between the encroachment by D obovata in grasslands and back fires. Ha = There is an association between the encroachment by D obovata in grasslands and back fires	0.05	2.716	0.099	Accept Ho
EN / FB	Ho = There is no association between the encroachment by D obovata in grasslands and the cutting of fire-breaks around forests and bush clumps Ha = There is an association between the encroachment by D obovata in grasslands and the cutting of fire-breaks around forests and bush clumps	0.05	1.313	0.251	Accept Ho
EN / IAPC	Ho = There is no association between the encroachment by D obovata in grasslands and the implementation of Alien Invasive Plant control programs Ha = There is no association between the encroachment by D obovata in grasslands and the implementation of Alien Invasive Plant control programs	0.05	1.111	0.292	Accept Ho
EN / BEC	Ho = There is no association between encroachment by D obovata into grasslands and bush encroachment by indigenous plants. Ha = There is an association between encroachment by D obovata into grasslands and bush encroachment by indigenous plants	0.05	0.208	0.648	Accept Ho
EN / BG	Ho = There is no association between D. obovata encroachment and the absence of Bulk Grazers in grasslands Ha = There is an association between D. obovata encroachment and the absence of Bulk Grazers in grasslands	0.05	4.444	0.035	Reject Ho Accept Ha
EN / MF	Ho = There is no association between D. obovata encroachment and the absence of Mixed Feeders in grasslands Ha = There is an association between D. obovata encroachment and the absence of Mixed Feeders in grasslands	0.05	4.444	0.035	Reject Ho Accept Ha

Key to abbreviations used in the table where 0 = No encroachment recorded, 1 = encroachment recorded

EN = encroachment by *D. obovata*.
FF(a) = Fire frequency annual
FF(b) = Fire frequency biannual
FS(a) = Fire season autumn
FS(w) = Fire season winter
FS(s) = Fire season spring
FI(hf) = Fire intensity - head fires
FI(bf) = Fire intensity - back fires
FB = Fire breaks maintained around forest
IAPC = Invasive Alien Plant Control programs
BEC = Bush encroachment control programs
BG = Bulk Grazers present
MF = Mixed Feeders present

Appendix 4. PCA results – Total Variance Explained. Results for encroachment of D. obovata into moist coastal grasslands in relation to reserve management practices.

Component	Initial Eigenvalues			Extraction sums of squared loadings			Rotation sums of squared loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	5.13	39.466	39.466	5.131	39.466	39.466	4.063	31.253	31.253
2	2.220	17.076	56.543	2.220	17.076	56.543	2.686	20.659	51.912
3	2.134	16.415	72.958	2.134	16.415	72.958	2.477	19.058	70.969
4	1.213	9.334	82.292	1.213	9.334	82.292	1.472	11.322	82.292
5	0.881	6.776	89.068						
6	0.596	4.585	93.653						
7	0.438	3.370	97.024						
8	0.187	1.435	98.458						
9	0.145	1.118	99.576						
10	0.055	0.424	100.000						
11	3.755E-16	2.888E-15	100.000						
12	1.111E-16	8.549E-15	100.000						
13	-2.160E-16	-1.661E-15	100.000						
Extraction Method: Principal Component Analysis.									

Appendix 5. Correlation Matrix of reserve management practices compared against recorded encroachment by *D. obovata*.

Correlation		EN	FF(a)	FF(b)	FS(a)	FS(w)	FS(s)	FI(hf)	FI(bf)	FB	IAPC	BEC	BG	MF
	EN	1.000	0.212	-0.212	-0.032	0.050	-0.010	-0.369	0.369	0.179	0.290	0.082	-0.522	-0.522
	FF(a)	0.212	1.000	-1.000	0.664	-0.302	-0.394	0.369	-0.369	-0.179	-0.522	0.533	0.058	0.290
	FF(b)	-0.212	-1.000	1.000	-0.664	0.302	0.394	-0.369	0.369	0.179	0.522	-0.533	-0.058	-0.290
	FS(a)	-0.032	0.664	-0.664	1.000	-0.367	-0.664	0.245	-0.245	-0.319	-0.787	0.685	0.303	0.545
	FS(w)	0.050	-0.032	0.302	-0.367	1.000	-0.452	-0.250	0.250	0.157	0.289	-0.153	0.000	0.000
	FS(s)	-0.010	-0.394	0.394	-0.664	-0.452	1.000	-0.034	0.034	0.179	0.522	-0.533	-0.290	-0.522
	FI(hf)	-0.369	0.369	-0.369	0.245	-0.250	-0.034	1.000	-1.000	-0.454	-0.192	0.272	0.192	0.019
	FI(bf)	0.369	-0.369	0.369	-0.245	0.250	0.034	-1.000	1.000	0.454	0.192	-0.272	-0.192	-0.192
	FB	0.179	-0.179	0.179	-0.319	0.157	0.179	-0.454	0.454	1.000	0.182	0.043	-0.018	-0.018
	IAPC	0.290	-0.522	0.522	-0.787	0.289	0.522	-0.192	0.192	0.182	1.000	-0.471	-0.467	-0.733
	BEC	0.082	0.533	-0.533	0.685	-0.153	-0.533	0.272	-0.272	0.043	-0471	1.000	0.471	0.471
	BG	-0.522	0.058	-0.058	0.303	0.000	-0.290	0.192	-0.192	-0.182	-0.467	0.471	1.000	0.733
	MF	-0.522	0.290	-0.290	0.545	0.000	-0.522	0.192	-0.192	-0.182	-0.733	0.471	0.733	1.000
This Matrix is not positive definite														

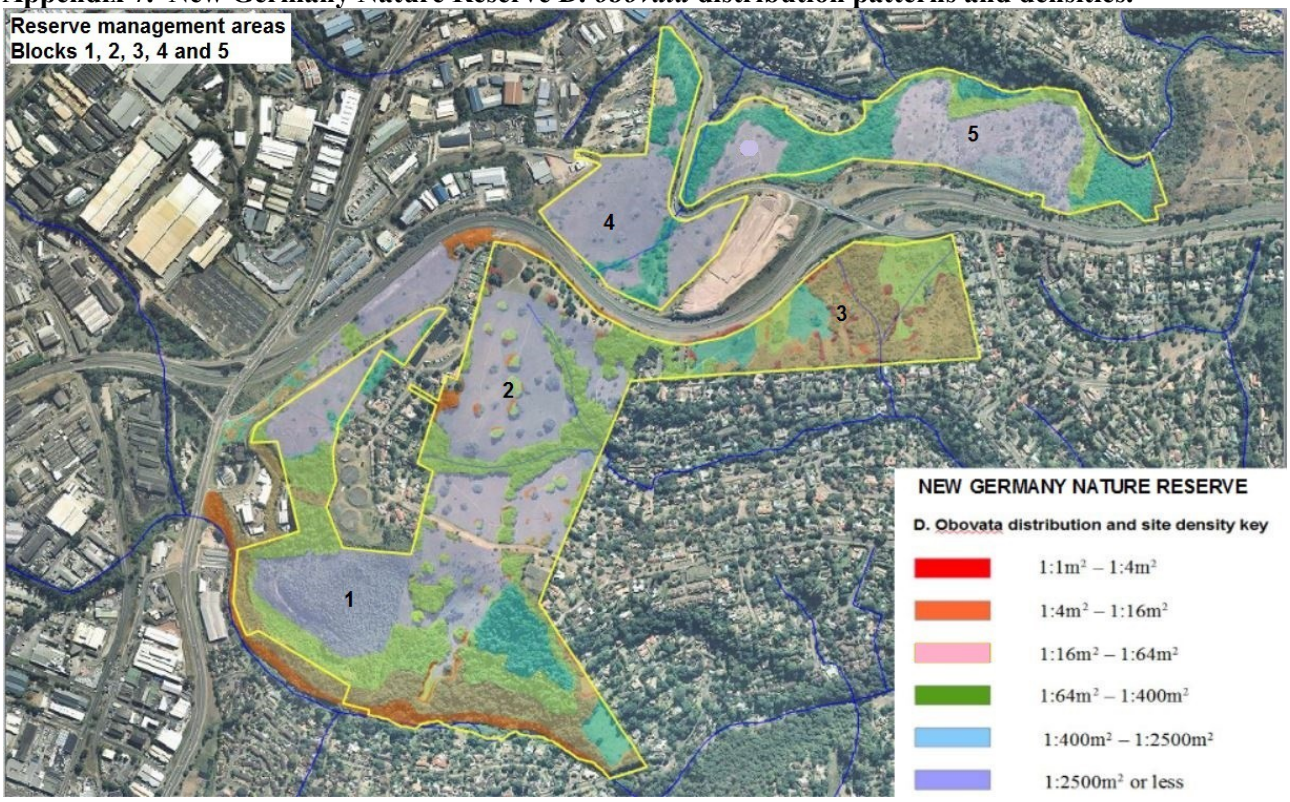
Key to abbreviations used in the table where 0 = No encroachment recorded, 1 = encroachment recorded

EN = encroachment by *D. obovata*.
FF(a) = Fire frequency annual
FF(b) = Fire frequency biannual
FS(a) = Fire season autumn
FS(w) = Fire season winter
FS(s) = Fire season spring
FI(hf) = Fire intensity - head fires
FI(bf) = Fire intensity - back fires
IAPC = Invasive Alien Plant Control programs
BEC = Bush encroachment control programs
BG = Bulk Grazers present
MF = Mixed Feeders present
FB = Fire breaks maintained around forest

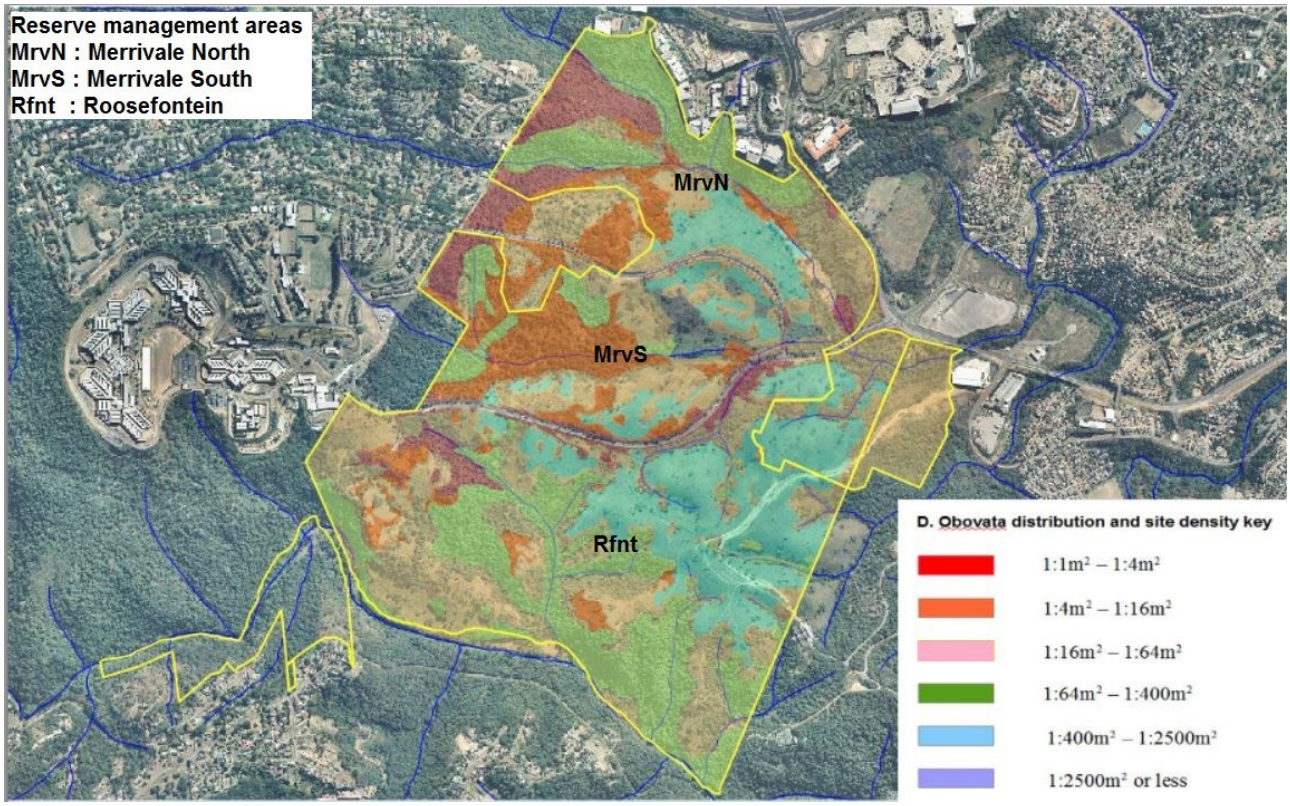
Appendix 6. Summary of the coverage of the nature reserve grassland areas by *D. obovata* recorded in the 2016/2018 field surveys compared to loss by bush encroachment for the categories 1:2m² - 1:4m², 1:4m² - 1:16m² and 1:16m² – 1:64m².

Reserve	Management block	Extent of grassland as at 1999	Grassland area gained or lost to bush encroachment and *D. obovata*	Grassland area encroachment by *D. obovata*	Percentage of grassland encroached by just *D. obovata*
Roosefontein	Roosefontein	598800m²	57225m² loss	307607m²	51.37%
	Merrivale North	220082m²	18708m² loss	114926m²	52.22%
	Merrivale South	178221m²	56997m² loss	171147m²	96.03%
New Germany	Block 1	82299m²	2679m² loss	4274m²	5.19%
	Block 2	125300m²	0.0m²	1900m²	1.52%
	Block 3	75941m²	35644m² (gain)	58119m²	76.53%
	Block 4 & 5	188939m²	3381m² loss	0.0m²	0.00%
Palmiet	Dawncrest grassland	2718m²	0.0m²	2681m²	98.64%
	Fuarea grassland	22754m²	2102m² gain	9956m²	43.75%
UKZN Westville	M19	88245m²	55831m² loss	32414m²	36.73%
	Eastern grassland	269370m²	97715m² loss	156475m²	58.09%
	Palmiet valley	5212m²	1275m² loss	3937m²	75.54%

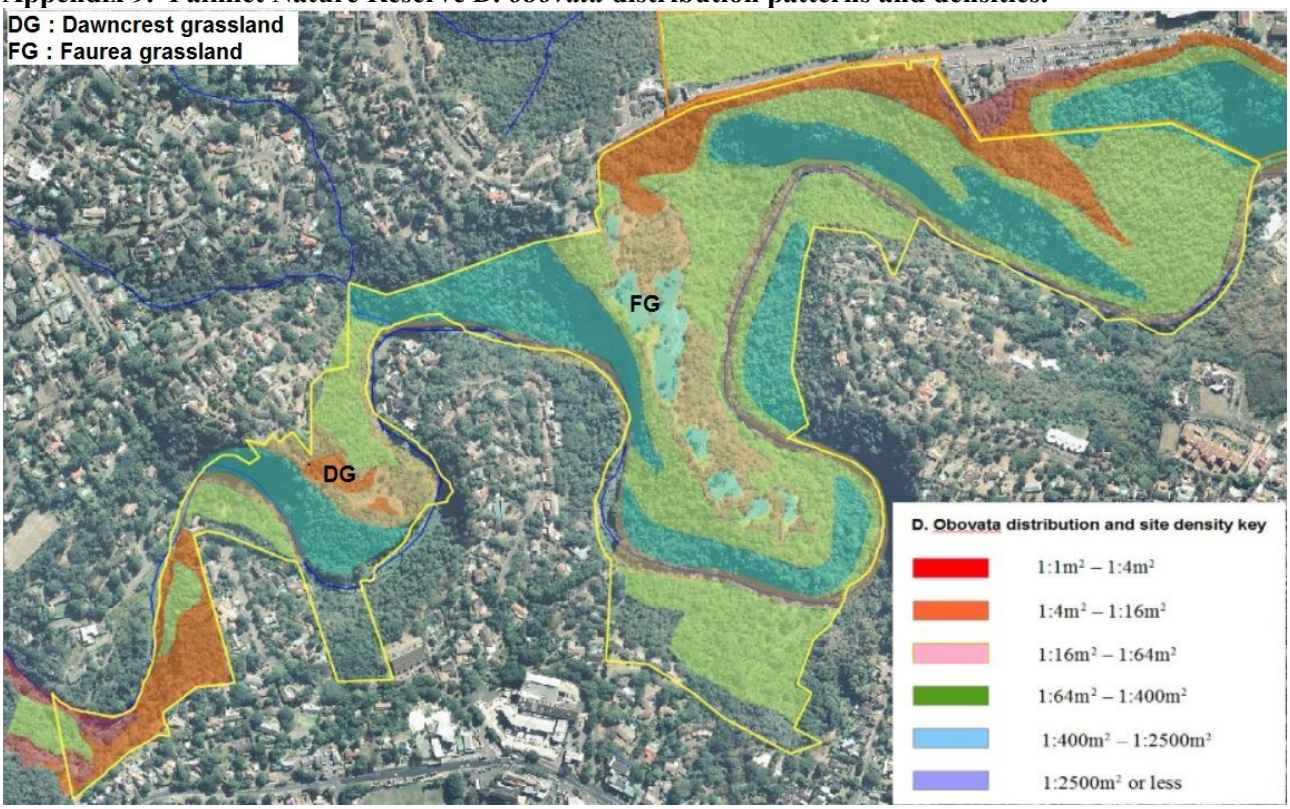
Appendix 7. New Germany Nature Reserve *D. obovata* distribution patterns and densities.



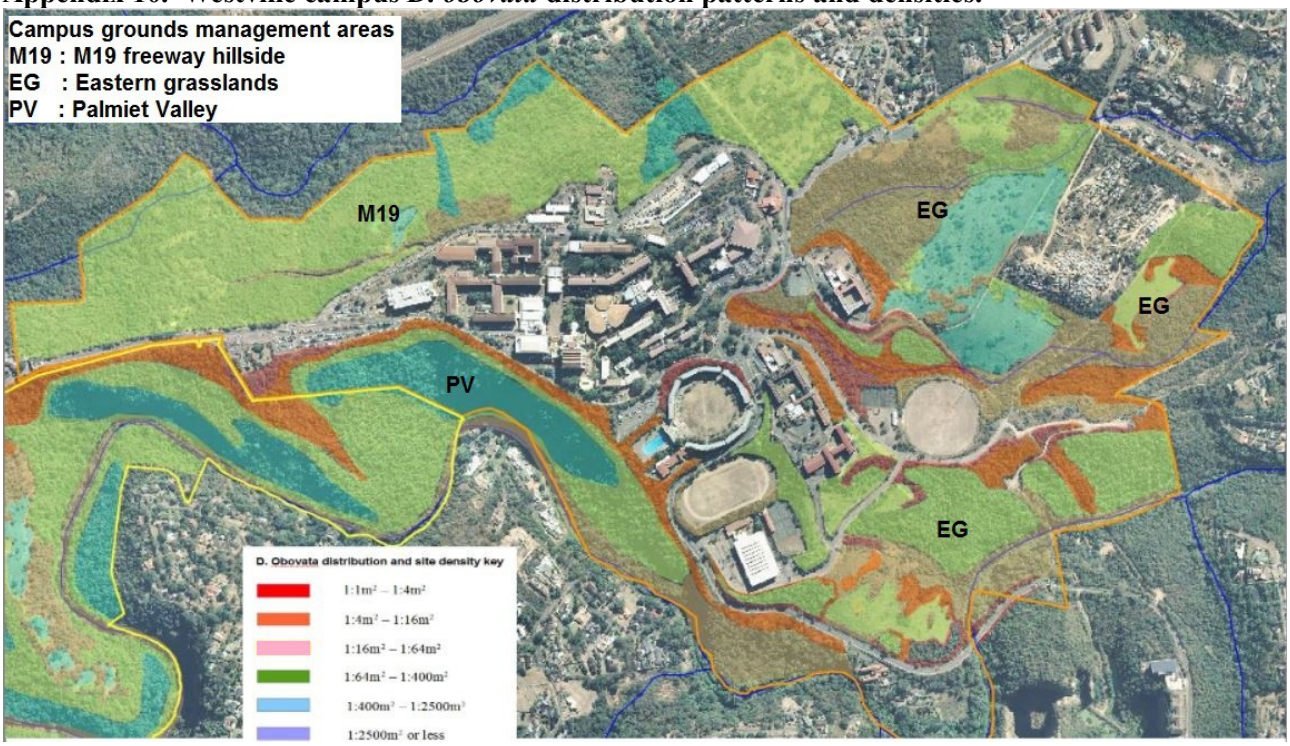
Appendix 8. Roosefontein Nature Reserve *D. obovata* distribution patterns and densities.



Appendix 9. Palmiet Nature Reserve *D. obovata* distribution patterns and densities.



Appendix 10. Westville campus *D. obovata* distribution patterns and densities.



Appendix 11. *D. obovata* occurrence at a density of 1:400m^2 – 1:2500m^2 within the grasslands at Roosefontein Nature Reserve.

Appendix 12. Stands of Gulliver plants at densities of 1:4m^2 – 1:16m^2 adjacent to a forest which has been over run by *D. obovata* at Roosefontein Nature Reserve.

Appendix 13. *D. obovata* encroaching into the grassland at Roosefontein Nature Reserve.

Appendix 14. Total coverage of 2.01ha of hillside at densities of 1:1m^2 – 1:4m^2 by *D. obovata* at Roosefontein Nature Reserve.

CHAPTER 3: **An assessment of the distribution of *Dalbergia obovata* diaspores from forest margins and post establishment vegetative propagation within adjacent grasslands**

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3.1 Abstract

Encroachment into the moist coast grasslands within Ethekwini Municipality by *Dalbergia obovata*, an indigenous species of forest liana which formed dense mono species stands that excluded all other plant species and did not appear to undergo self-thinning, was identified as a potential biodiversity threat. Identification of the mechanisms of *D. obovata* diaspore dispersal from neighbouring adjacent forests and subsequent patterns of propagation within the grasslands was required to understand how *D. obovata* encroached into the grasslands. A simple wind dispersal model for D. *obovata* diaspores was developed and compared against the historic orthophoto records of two nature reserves. Field surveys were also undertaken to map the distribution of plants within stands of *D. obovata* in the grasslands of the study areas and to investigate the primary methods of propagation by *D. obovata* once it had become established. The results of the wind dispersal modelling and field surveys showed that *D. obovata* dispersal was a product of the height of host trees and wind velocity but for successful dispersal to occur *D. obovata* had to occupy a position close to the forest margin. Successful establishments of *D. obovata* were infrequent but a resistance to grassland fires and clonal propagation from the roots and lateral branches resulted in a constant expansion of the stands and accounted for the lack of evidence of self-thinning. The progressive expansion of the stands in the grasslands was confirmed as representing a threat to the grasslands.

13.2 Introduction

Encroachment of grasslands by woody plants has been reported globally (Naito and Cairns, 2011) and has been attributed to a combination of universal drivers such as an increase in atmospheric CO_2 (Wigley et al., 2009) and local conditions (Devine et al., 2017, Joubert et al., 2012) such as mean annual precipitation, overgrazing and veld management practices. A similar global increase in the occurrence of lianas in forest canopies has also been recorded (Laurence et al., 2011, Philips et al., 2002, Gallagher and Leishman, 2012, Yorke et al., 2013). As with woody species associated with encroachment of of grasslands, the increased growth rate of liana growth and expansion has been attributed to the global increase of CO_2 (Zotz et al., 2006)), together with local habitat disturbances (Schnitzer and Bongers, 2011, Yorke et al., 2013) which have provided opportunities for lianas to take advantage of increased forest margins. Estimation of liana population increases in forests have varied according to the methods used. (Schnitzer and Bongers, 2011), recorded a doubling in stem counts and basal stem area with an associated increase in biomass, whereas other researchers such as Philips et al (2002), recorded increases in canopy cover from 33% to 75% of the canopy area.

Studies on the distribution of lianas within the Amazonian forest estimated that lianas comprised up to 33% of tropical forests (Yorke et al., 2013) but that there is a relationship between the frequency of liana stems and basal area relative to the increased distance inwards from the edge of the forest (Laurence et al., 2001), with a decrease in the number of plants in response to an increased distance. Conversely the average basal stem diameter of increased with distance inward from the forest edge and plant age. This was confirmed by Londré and Schnitzer (2006), who also concluded that there was a marked decrease in liana density towards the centre of forests. It is suggested that these spatial patterns of lianas within forests were also in response to habitat fragmentation and increased forest margins as opposed to elevated CO_2 or climate change and that lianas appear to benefit from habitat fragmentation and the associated increase in forest edges (Londré and Schnitzer, 2006, Arroyo-Rodríguez and Toledo-Aceves, 2009).

Schnitzer and Bongers (2011), cited four methods of propagation utilised by lianas to cover gaps in the forest canopy; (i) seed dispersal and germination, (ii) advanced regeneration of damaged stems, (iii) lateral growth of branches along the forest floor with rooting and generation of vertical growth and (iv) long distance clonal

recruitment via vines in the canopy which fall to the ground and then take root. Yorke et al (2013), confirmed that a large percentage of liana recruitment in old forest areas that was disturbed by logging operations was via long distance clonal colonisation, specifically from the re-rooting of fallen vines and that large lianas can extend in a radius of up to 500m from their main stem or trunk. Available literature (Coates Palgrave, 1977, Pooley, 1993), describes D. *obovata* as a liana or creeper which scrambles through forest canopies but which can also occur as a tree that attains a maximum height of 6m both in the wild or as a cultivated shrub. The analysis of the reserve management practices and records of *D. obovata* encroachment into the grasslands from seventeen conservation areas within the eThekwini Municipal area were confirmed by detailed ground level surveys which showed that *D. obovata* was encroaching into the grasslands with up to 43% of the grassland in some reserves having been encroached (Stewart et al., submitted). *D. obovata* is capable of forming dense mono species stands within grasslands with stands covering up to 2 ha in extent (Stewart et al., submitted). The threshold level at which encroachment becomes self-propagating unless the underlying drivers of encroachment are removed is approximately 18% to 20% (Loehlel et al., 1996) and if *D. obovata* is establishing in grasslands it could be considered as an emerging bush encroachment species.

The process of self-thinning or Yoda's $^{-3}/_{2}$ power rule, is widely accepted as a general law and describes the process of natural plant mortality and reduction of plant densities in response to canopy contact mortality and competition for resources (Zeide, 1987, Wiegand et al., 2008) and has been shown to operate consistently across a wide range of conditions (Reynolds and Ford, 2005) from high density stands of short lived annuals such as *Impatiens capensis* to long lived *Pseudotsuga menziesii* where self-thinning occurs between the ages of 800 and 1200 years. Although this study did not investigate the application of the self-thinning law to the growth and propagation of *D. obovata* it was noted that no evidence of canopy contact mortality was observed in either the field surveys or the historic orthophotos.

Relatively little is known about *D. obovata* as a species other than general information which describes it as a climber that uses tendrils, its flowering and fruiting times, and taxonomic information however the detailed phenology of *D. obovata* in terms of its complete life cycle including it's reproductive strategies is largely unknown. Anecdotal evidence (Nichols, 2017) suggests that seeds first need to be removed from the seed pods and scarified, and that fresh seed needs to be used in order for successful germination in a nursery

environment nursery. No studies have been undertaken to determine scarification is required in the natural environment, what the possible agents responsible for scarification would be or even how the seed dispersal takes place.

The survival and spatial distribution of organisms with a sessile adult phase of their life cycle depends on having mobile seeds, spores, eggs or larvae (Pergl et al., 2011). It then follows that the spatial dynamics (Levin et al., 2003) and the long term survival of any plant species depends on the probability of their seeds or other reproductive tissues (Klein, 1999, Vivian-Smith et al., 2007), reaching a suitable medium for germination or growth and subsequent recruitment of seedlings into the adult population (Greene and Johnson., 1989, Levin et al., 2013).

Dalbergia obavata seeds are small kidney shaped beans with an average length of 6.5 mm and a mass of 0.0764 grams (T. Stewart, unpublished data). The measured seed pods could be generally described as elongated, flattened and tapered at the base and apex with either a single seed contained at the approximate mid-point or a pair of seeds contained at the 1/3 and 2/3 position along the length of the seed pod. Single seed pods averaged 40mm in length and double seed pods averaged 57mm in length and the width of the pods is a fairly consistent 11mm (Appendix 1) for both single and double seed pods. The general morphology of the seed pod conforms to descriptions of wind dispersed winged seeds or samaras (Norberg, 1973, Burrows, 1975). No separation of the seed pod and release of the seeds has been recorded and for the purposes of this investigation it was assumed that the seeds of *D. obovata* are dispersed together with the pods and are therefore referred to as diaspores (Matlack, 1987). *D. obovata* occurs in a wide range of densities of different sized individuals in grasslands adjacent to forests (Stewart et al., submitted). The assumption therefore is that although diaspore dispersal has not been observed, it does occur and based on the diaspore morphology, it is most probably via wind dispersal.

Secondary dispersal may also account for the final dispersal patterns of seeds (Schurr et al., 2005) through accidental dispersal by species which predate on seeds such as insects and rodents (Forget and Milnerton, 1991, Milesi and Lopez De Casenave., 2004., Wall, 2008). Seed removal does not however automatically equate to seed predation or consumption (Vander Wall et al., 2005). Elaiosome-bearing seeds use ants as

vectors (myrmecochory) for seed dispersal (Whitney, 2002), but examples also exist of fungus farming ants harvesting seed pods of non-myrmecochoric tree species with the removal of seeds from the pods inside the ant nests (Milesi and Lopez De Casenave, 2004). The evolution of fungus farming in new world ants (Meuller et al., 2001), is paralleled by the evolution of fungus farming termites in Africa and Asia (Aanen and Boomsa, 2006, Aanen and Eggleton, 2005), but no records were found of secondary dispersal through seed pod harvesting by termites.

In order for *D. obovata* to successfully encroach into grasslands from adjacent forests or bush clumps the diaspores must be successfully distributed beyond the forest boundary and once germinated, plants must be capable of successfully expanding and competing with grass species for resources such as water, nutrients and light (Riginos., 2009, Moustakas et al., 2013). Three questions were therefore raised concerning *D. obovata* distribution and propagation: (1) how far are *D. obovata* diaspores carried by wind into the grasslands, (2) is there a critical position that the parent plant must occupy on the host tree's canopy in order for diaspores to escape the forest boundary, (3) how does *D. obovata* grow and propagate once established in the grassland.

3.3 Methods

Two approaches were employed to investigate the dispersal of diaspores beyond the boundaries forests adjacent land and the subsequent expansion of stands of *D. obovata*. The first method was the development of a simplified ballistics chart for the dispersal of diaspores under different wind strengths and its application to positions on the host plant's canopy. The second method entailed the mapping of plants within *D. obovata* stands in grasslands and the analysis of historical ortho photos as well as the investigation of any evidence of vegetative propagation.

3.3.1 Diaspore Dispersal

Analysis of the terminal velocities of diaspores and predicted wind drift in regard to distance from the canopy edge

Two alternative methods were considered for the modelling of wind dispersal of *D. obovata* diaspores. These

were the direct observation method and ballistics modelling. The direct observation of seed dispersal and mapping of seed dispersal is done by either observing the flight of seeds in the field or recording the number and location of seeds found in the field in reference to a known parent plant or by using seed traps placed in specific patterns of direction and distance from a known seed source (Bullock and Clarke., 2000, Nathan et al., 2002). Most seeds tend to fall within short distances of the parent plant with long distance seed dispersal generally considered as distances over 100m (Cain et al., 2000) but becomes increasingly less accurate as distance increases, (Levin et al., 2003). “Non-buoyant particles of different materials like seeds and fruit supported by aerodynamic forces always move relative to the air when in flight”, (Burrows 1975, page 405). During free-fall in still air, all objects will experience gravitational acceleration until the force exerted by gravity is balance by the upward pressure of the air as a result of aerodynamic drag and a steady terminal velocity is reached. The aerodynamic drag is a product of the objects velocity, density, cross sectional surface area and the air density or wind pressure constant (Burrows 1975). The same principal can be applied to the lateral acceleration of seeds until the horizontal wind velocity is reached. Indirectly it means that the drag can be calculated for an object of a known mass in free fall in air by comparing the point at which terminal velocity is reached with the theoretical velocity of the same object in a vacuum. Once the drag is known the effective aerial buoyancy and volume can be calculated.

Simple ballistics models used for the calculation of single projectile trajectories consider the launch angle, muzzle velocity, ballistic coefficient, drag and gravitational attraction (Jauhari, 1986). Indirect methods of predicting seed or diaspore dispersal tend to be mechanistic models which integrate ballistics formulas with statistical components to describe patterns of seed dispersal under varied conditions or phenomenological models which describe seed dispersal and can be incorporated into mechanistic models (Levin et al., 2003). The simplest of these models describing anemochoric dispersal of seeds are based on ballistics formulas with the most important variables being horizontal wind speed, the release height of seeds and terminal velocity of the seeds (Marion and Ohanian, 1979, Burrows, 1975, Greene and Johnson, 1989). More precise modelling requires the inclusion of wind turbulence, vortex shedding and storm events (Cain et al., 2000, Nathan et al., 2002, Soons., et al., 2004, Tackenberg et al., 2003), which can greatly extend the range of seed dispersal. The inclusion of statistical calculations is required when dealing with multiple seeds which exhibit a degree of

randomness resulting from a combination of variables such as individual release heights, variances in diaspore morphology, wind speed and turbulence (Cain et al., 2000, Nathan et al., 2002, Soons., et al., 2004, Tackenberg et al., 2003).

In the case of *D. obovata* however, there are no records of the mass release of diaspores from parent plants or corresponding recovery of diaspores from the field. This necessitated the use of a simplified ballistics model for the calculation of the theoretical flight path of the diaspores. Most models of seed dispersal assume an instantaneous horizontal wind velocity and terminal velocity (Soons., et al., 2004, Tackenberg et al., 2003) and is convenient when calculating seed dispersal over long distance when released from tall trees. This assumption could however introduce inaccuracies when considering that the release heights of diaspores from a parent plant above the host tree canopy may be measured in centimetres and determination of the distance of the parent plant inward from the canopy which may be critical to the successful dispersal of diaspores beyond the forest margin.

Mature, dried *D. obovata* diaspores were collected at random from trees adjacent to survey site 1C at Marian Wood Nature Reserve of which one hundred selected at random and then measured, weighed and dropped individually from a height of 4.5m in a still air environment against a graduated backdrop. The backdrop was marked in vertical increments of 0.25m and the diaspores descent was filmed using a Fuji Film S4300 14 mega pixel camera with a 35mm wide angle lens at 30 frames per second. The videos were then analysed using Adobe Premier PRO CC 2015.5 which allowed the flight times of the diaspores to be viewed at 10% speed at 308.7 frames per second in sequentially numbered frames. The results were captured into a spreadsheet which allowed the frames per height increment to be converted to ms^{-1} and the average initial rates of vertical acceleration, the point at which average terminal velocities were attained and other ballistics data to be calculated by entering the formulas into the spreadsheet. The difference between the terminal velocity and the theoretical velocity in a vacuum for the same height and the wind pressure constant was used to calculate the average cross sectional area of the diaspores in flight. This was then used to calculate the average rate of horizontal acceleration during free fall under different theoretical wind strengths and the corresponding time and distance travelled before wind speed was reached and the average angle of descent. Microsoft PowerPoint 97/2000 XP was then used overlay the final diaspore trajectories under varying

theoretical wind speeds over a background grid drawn on a photo of a tree with a rounded crown shape that was growing in the grassland at Marian Wood Nature Reserve and which was covered with *D. obovata* and mature *D. obovata* diaspores.

The standard equations of motion, force and pressure used for the ballistics calculation were;

$$\mathbf{V = U + s / t} \quad (3.3.1.1)$$

$$\mathbf{s = ut + ½ at^2} \quad (3.3.1.2)$$

$$\mathbf{V^2 = U^2 + 2as} \quad (3.3.1.3)$$

$$\therefore \quad \mathbf{V_{(0.25m)} = S / t_{(0.25m)} = S / (\sum(fr / frs^{-1}) / n \quad = 0.25 / \sum(fr / 308) / 100} \quad (3.3.1.4)$$

$$\text{and} \quad \mathbf{a_{(0.25m)} = \Delta V_{(0.25m)} / t_{(0.25m)} \quad = (V - U) / t} \quad (3.3.1.5)$$

$$\mathbf{P = F/A = (m \times a)/A} \quad (3.3.1.6)$$

$$\mathbf{V_d = (V - U) / t = (Pw \times A) / m} \quad (3.3.1.7)$$

where Horizontal displacement $= \mathbf{V_d \times t_{(h)}}$ (3.3.1.8)

and the angle of decent is $= \mathbf{\tan^{-1} (s_{(h)} / s_{(w)})}$ (3.3.1.9)

Where **V** = final velocity

U = initial velocity

s = distance

t = time

$\mathbf{V_{(0.25m)}}$ = average diaspore velocity per 0.25m vertical height increment in = ms^{-1}

$\Delta \mathbf{V_{(0.25m)}}$ = difference in velocity between 0.25m height increments = ms^{-1}

$\mathbf{V_t}$ = terminal velocity

$\mathbf{V_d}$ = horizontal diaspore velocity

$\mathbf{a_{(0.25m)}}$ = acceleration = ms^{-2} and where acceleration in a vacuum is 9.8 ms^{-2}

$\mathbf{s_{(h)}}$ = release height

$\mathbf{s_{(w)}}$ = horizontal wind displacement

$\mathbf{s_{(0.25m)}}$ = vertical height increments of 0.25m

$\mathbf{t_{(0.25m)}}$ = average fall time of diaspores per 0.25m height increment in seconds = s

$t_{(h)}$ = time of free fall from release height

fr = number of frames per 0.25m height increment

P = pressure

F = force Newtons = kg ms^{-2}

m = mass kg

A = cross sectional area = m^2

P_w = wind pressure constant = 2.56 x 10^{-3} Nm^2

Testing for secondary seed dispersal of *D. obovata* diaspores.

A set of six wire mesh baskets was set out at Marian Wood nature Reserve at site 1C. Two baskets were placed 5m inside the edge of the forest, two baskets were placed among the vegetation in the forest/grassland ecotone and remaining two baskets were placed 5m into the grassland. A total of one hundred dried D. obovata diaspores were placed in each basket to prevent them from being blown away by the wind and inspections and counts of the diaspores in each basket was done on a weekly basis for the months of January 2017 to June 2017. If diaspores had been removed from the baskets it was recorded and the number topped up and monitored.

3.3.2. Mapping of individual stands of *D. obova*ta and comparison against historic GIS data

Field mapping exercises were undertaken of stands of *D obovata* in three grasslands within two nature reserves that were identified from available reserve management records and preliminary surveys of *D. obovata* encroachment (Stewart et al., submitted). Two of these were at Marian Wood Nature Reserve and the third at the Treasure Beach Grasslands Reserve.

Marian Wood Nature Reserve

Survey site 1C, (29º 50' 116.9" S, 30º 50' 29.1" E), was located in a small but species rich portion of grassland on the top of a hill and survey site 2A (29º 50' 19.7" S, 30º 50' 27.4" E), was located in a low lying grassland in a valley bottom.

The two survey grids were set up in March 2012 to cover all visible D. obovata plants in the stands. A 60m x 40m grid was set up at survey site 1C and a 30m x 30m grid at site 2A. Due to the smaller size of the *D. obovata* stand at site 2A a smaller survey grid was adequate. Permanent concrete posts were placed on the corners of the 20m grids as reference points for follow up surveys. The canopy was removed in order to expose the stems for accurate mapping. All of the stems were were cut 10cm above the ground and a herbicide was applied after which stainless steel tags were attached for future identification. This was done in order to allow differentiation in follow up surveys between original mapped plants which may have regrown and new seedlings. The tagged stems were then mapped in 1.0m x 1.0m squares and captured onto a GIS map. The sites were resurveyed in June 2015 and again in September 2016 to check the accuracy of the tagged plants to be used as reference points for comparison of the available historic ortho photos from 1999 to 2016. A second survey was then undertaken at site 1C and 2A in October 2016 to establish if *D. obovata* used clonal propagation from the roots. This entailed the excavation and mapping of the course interconnecting roots of all plants that were tagged during the first survey. Monthly site inspections were continued until September 2018 and any new seedlings were mapped as a new layer on the GIS project using the available 2016 backdrop. The accurate mapping of all plants from all surveys and capturing as individual layers per survey allowed for the positions of all surveyed plants to be superimposed onto the visible stands of *D. obovata* in the historical orthophotos and enabled the year in which stands were first established to be identified, the rates of expansion until they were treated with herbicide and identification of any new plants that became established after the initial herbicide application. The most probable parent plants were also identified by mapping the predominant wind directions at each site and identification of any mature *D. obovata* plants in the forest canopy relative to the *D. obovata* stands along the prevailing wind lines. On completion of the field surveys the stems of the potential parent plants at site 1C which were identified along the prevailing wind lines were cut and treated with 5% picloram in order to prevent further encroachments. The parent plant at site 2A was not cut and treated initially because the host tree was broken during a storm leaving only the trunk with the main stem of the *D. obovata* vine still attached. This plant subsequently regenerated and was then cut and treated during a follow up survey in June 2015.

Treasure Beach Grasslands Reserve (29° 56' 39.25" S, 30° 59' 53.00” E).

An initial survey was conducted in September 2016 at the Treasure Beach grassland where the perimeters of

two distinct stands of small *D. obovata* seedlings were recorded and against which any subsequent expansion could then be measured. The grasslands were re-surveyed in September 2018 to assess the spread of *Dalbergia obovata*. During the second survey other indigenous woody encroaching species were also included to provide input into thee review of the reserve management plans.

Two permanent concrete survey posts were placed along the North - South axis through the centre of the grassland in line with a survey beacon. A permanent boardwalk on the perimeter of the grassland was also measured off and marked at 10m intervals as reference points. The approximate boundaries of the stands of encroaching species were marked with poles and a series of fixed point photographs were taken from the survey posts. The boundaries of the encroaching species and position of individual plants were recorded relative to the survey posts and boardwalk and the results captured as a GIS layer against the available 2016 backdrop. The distribution of *D. obovata* was then compared with the distribution recorded two years previously.

3.4 Results

3.4.1. Diaspore dispersal

Analysis of the terminal velocities of diaspores and resulting wind drift

Analysis of the videos of diaspores dropped against a backdrop marked off in 0.25m increments established that the initial rate of acceleration reached a maximum of 5.77ms^{-2} at 0.25m of fall and then decreased until the terminal velocity of 1.95ms^{-1} was reached at approximately 1.0m of fall (Appendix 2). This corresponded to the average distance at which diaspores either began to rotate along their axis, spun in a helical manner or did both at the same time. This behaviour was erratic with diaspores displaying a range of motion ranging from the helical spiralling of non-rotating diaspores around a vertical axis of descent to the rotation of diaspores with a corresponding increase in lateral motion. Diaspores were observed to stop and start rotating during free fall and even reverse their direction of rotation. Fluctuations in terminal velocity (Appendix 2) were also recorded and necessitated that the average rates of acceleration and terminal velocity had to be used. The velocity difference at 1.0m between free fall in an atmosphere and free fall in a vacuum was calculated at 2.49ms^{-1} and the corresponding longitudinal cross sectional area of the diaspores was

approximately 0.088 mm^2 which gave an average cross sectional density of 0.868 gm^{-2}. By applying the wind pressure constant it was determined that regardless of the horizontal wind strength the diaspores achieved wind speed within 0.34s which corresponds to a fall height of 0.5m (Appendix 3). The horizontal displacement of diaspores under varying release heights and wind velocities (Appendixes 4 and 5) records that an increase in wind velocity or release height shows a corresponding linear increase (Appendix 6) in the distance which diaspores are transported with distances of up to 85m for tree heights of 10m and winds of 60.0km hr^{-1}. The horizontal displacement for a wind speed of 60km hr^{-1} corrected for initial acceleration for a wind speed of 60.0km hr^{-1} provides a difference of 1.7m when compared with the assumption of instantaneous velocity for the same wind speed which equates to a corresponding lateral shift of the release point closer to the edge of the canopy. As the wind speed increases there is also a decrease in the angle of descent of diaspores (Appendixes 7 and 8). Overlaying the diaspore trajectories on a photo of a tree crown (Appendixes 9, 10 and 11) with a 1:1 grid shows that at a wind speed of 15.0km hr^{-1} a diaspore would need to be positioned within 0.5m of the edge of the canopy in order to escape. If the distance is greater than that then the diaspores will descend into the canopy before they are blown clear of the canopy edge. As the wind speed increases the distance to the edge of the canopy also increases with the critical distance for a wind speed of 60.0km hr^{-1} being approximately 1.0m. The distance of the *D. obovata* stands from the identified parent plants (Appendixes 12 and 13) indicate that diaspore dispersal for six of the eight stands at Marian Wood Nature Reserve occurred with wind speeds of between 30.0km hr^{-1} and 51.0km hr^{-1}, one stand was consistent with a wind speed of 9.0km hr^{-1} and the shape of the 2018 stand at site 1C was consistent with wind speeds varying between 24.0km hr^{-1} and 92.0km hr^{-1}. Although theoretical wind speeds were used for the development of the wind dispersal model, wind speeds at Marian Wood Nature Reserve during a storm event on the 17th October 2017 were measured with a Kestrel hand held anemometer serial No. 2278445 and reached 89km hr^{-1} (Appendix 16).

Testing for secondary seed dispersal.

A single episode of foraging of the diaspores in the seed baskets was recorded from the 2nd May 2017 to the 5th May2017. During this time period the diaspores were actively harvested by an unidentified species of harvester termite (Appendix 13). No other incidents of foraging or removal of diaspores from the baskets was recorded.

3.4.2 Mapping of the establishment of individual stands of *D. obovata* and comparison against the historic GIS data

Cutting and removal of the aerial portions of the *D. obovata* plants during the initial survey and mapping exercise at survey sites 1C and 2A at Marian Wood nature Reserve (appendix 14), revealed that what was originally considered to be a single stand covering most of site 1C was actually four separate stands of plants (Appendix 15). At site 1C a single potential adult D. *obovata* plant was identified scrambling through the forest canopy on the South side of the stand (Appendix 17). At site 2A a single potential parent plant was identified growing in the canopy of a large *Ficus natalensis* to the North of the stand (Appendix 16). It was also noted during this exercise that no other plant species were recorded in stands where *D. obovata* canopies had achieved 100% canopy cover. Comparison of the GIS map of the positions of plants recorded at sites 1C and 2A against the available historic ortho photos from 1999 to 2015 allowed the sequence of the establishment of *D. obovata* stands to be identified and recorded (Appendices 15, 16 and 17). At site 1C (Appendix 15 and 17) *D. obovata* successfully established in the grassland in 2002, 2006 and 2018. Successful establishments at site 2A (Appendix 16 and 17) took place in 2003, 2008 and 2015. Following the cutting and treatment of the identified probable parent plants at site 1C in 2012 and at site 2A in 2015 there were no further recruitments of *D. obovata* into the grasslands until a new stand of seedlings was recorded at site 1C in 2018. On investigation a new *D. obovata* vine was identified on the edge of the forest canopy at site 1C close to where the original parent plant was treated in 2012. This plant was surveyed and was found to be on the same North East and South West predominant wind line for the new stand of plants at site 1C (Appendix 15 and 17). Rates of expansion of *D. obovata* stands once established (Appendix 18) showed an average increase in stand diameter of 2.5m per year and it was also recorded that controlled grassland burns were conducted from 2002 to 2015 (Appendix 18). No trace of the plants visible in the new stand at site 2A in the 2008 ortho photo was found during the field survey and mapping exercise in 2012.

The excavation of the roots of *D. obovata* plants in site 1C and 2A revealed that the plants within distinct stands were connected to the same root network which formed a radial branched structure which connected to a single central plant (Appendixes 19 and 20). The central plants of each stand corresponded to the first plant visible in each stand in the chronological sequence of ortho photos. Rooting of lateral branches was not observed at Marian Wood Nature Reserve but it was recorded during the *D. obovata* survey at the Treasure

Beach Grasslands Reserve in September 2018 (Appendixes 22, 22, 23 and 24) where the radial lateral branches growing along the ground were measured at an average of 6.6m with the longest recorded as 10.2m with a diameter of 16.2m at its widest point and covered an area of 132m^2. This plant was not recorded in the 2016 survey and averaged an annual radial expansion of 4.0m per year.

3.5 Discussion

The results of the *D. obovata* diaspore wind dispersal modelling (Appendixes 4, 5 and 6) confirmed that the horizontal displacement of diaspores was a product of wind velocity and the vertical height from which the diaspores were released. The fluctuations in the terminal velocities (Appendix 2) were attributed to the erratic rotation and helical circling of the diaspores which could have caused changes in aerodynamic buoyancy (Burrows, 1975), due to a combination of the initial angle of the diaspore relative to the vertical when released and variations in the surface structure and shape of the diaspores. The results also confirmed that the assumption of instantaneous terminal velocity and wind velocity (Appendix 6) resulted in variances in the calculation of horizontal wind displacement when the release heights were less than 0.5m (Appendix 4) and changed the calculated distance back from the edge of the canopy at which diaspores could be released and effectively escape the forest fringe without falling into the canopy of the host trees. This distance was determined by a combination of canopy shapes and wind strengths which caused a change in the angle of decent of the diaspores. As wind velocities decreased (Appendixes 7, 8, 9, 10 and 11) the critical release point of diaspores moved closer to the edge of the canopy and for wind speeds below 15.0km hr^{-1}, plants needed to be positioned on the edge of the host trees canopy to allow effective diaspore dispersal. The ballistics table (Appendix 5) also confirmed that once diaspores escape the canopy they could be transported distances of up to 80m into the grasslands by strong winds.

The single episode of foraging on diaspores by termites was not repeated and provided insufficient data to indicate if it was secondary seed dispersal or opportunistic seed predation.

The mapping of plants at site 1C and 2A at Marian Wood Nature Reserve and the Treasure Beach Grasslands Reserve and comparison with historical ortho photos showed that successful establishments of *D. obovata* in the grasslands in relation to any particular parent plant in the forest canopy is an infrequent event. However

once *D. obovata* does become established it is capable of spreading at a continuous rate and is not controlled through the application of planned grassland burns. At site 2A there were three events over a 12 year period of which only one was confirmed by the field survey. At site 1C five separate stands were established over a sixteen year period. The tagging and mapping of individual plants in 2012 ensured that survivors of the herbicide applications could be correctly differentiated from newly germinated plants. The available information pertaining to the germination of *D. obovata* seed in a nursery (Nichols, 2017) suggests that *D. obovata* seeds do not remain viable for extended periods in the field and new plants recorded at intervals varying from three to six years after the herbicide applications were completed were unlikely to have been from seed that had lain dormant in the soil. They were more likely to have been released from the parent plant at site 2A that was broken during the 2012 storm and which subsequently regenerated and from the new parent plant identified at site 1C in 2018. Air bourne diaspores move according to the wind direction when in flight (Burrows, 1975) and will gravitate to the ground along the path of the wind flow. The lack of subsequent establishments along the predominant wind lines between the forest canopy and survey sites after the parent plants were treated with herbicide at site 1C in 2012 and at site 2A in 2015 suggests that these plants were correctly identified as the source of the diaspores from which the stands were established (Appendixes 15, 17 and 18) and supports the assumption that *D. obovata* diaspores are wind dispersed.

The excavation of the *D. obovata* roots at Marian Wood NR and the identification of rooting from lateral branches recorded at the Treasure Beach Grassland Reserve confirmed that *D. obovata* spread via clonal propagation following successful establishment within the grasslands. This suggests that all of the plants comprising the individual stands mapped at Marian Wood NR and Treasure Beach Grasslands Reserve were in fact genetically identical aerial portions of single plants. This then explained how *D. obovata* can form large dense continuously expanding stands within the grasslands without any evidence of canopy contact mortality taking place.

13.6 Conclusions

The results of the calculation of basic ballistics data for *D. obovata* diaspores and the comparison against stands of plants surveyed in the field supports the assumption that *D. obovata* dispersal is anaemochoric and that the distance at which diaspores are dispersed depends on the site specific combinations of prevailing wind speeds and the height of the plant in the host trees canopy. The successful dispersal of the diaspores beyond the forest boundary for an average range of wind speeds into adjacent grasslands is also dependent on the diaspores being released from a position not greater than 1.5m from the edge of the host trees canopy and that this critical release point shifts closer to the canopy edge as wind speeds decrease. The field survey records also showed that once *D. obovata* was successfully established in a grassland the plants were resilient to grassland fires, that the stand exhibited a constant rate of lateral expansion and that the primary method for expansion was clonal propagation from the roots and rooting of lateral branches. The confirmation of clonal propagation explained the lack of evidence of canopy contact mortality or self-thinning within large dense stands of *D. obovata* and which also enabled it to establish large constantly expanding stands which excluded other plant species. The implication is that although establishment of *D. obovata* stands in the grasslands from any single parent plant is an infrequent event, once established there is a continuous increase in encroachment which has the potential to transform the botanically rich moist coast grasslands within the urban nature reserves of Ethekwini Municipality into mono species stands of *D. obovata*.

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13.9 Appendices to chapter 3

Appendix 1. *D. obovata* diaspores showing single and double seeded pods.

Appendix 2. Average velocity and acceleration of diaspores as per 0.25m of vertical height travelled (red font indicates negative acceleration with a maximum velocity of 2.24ms^{-1}).

Height increments (m)	0.00m to 0.25m	0.25m to 0.50m	0.50m to 0.75m	0.75m to 1.00m	1.00m to 1.25m	1.25m to 1.50m	1.50m to 1.75m	1.75m to 2.00m	2.00m to 2.25m	2.25m to 2.50m	2.50m to 2.75m	2.75m to 3.00m	3.00m to 3.50m	3.50m to 3.75m	3.75m to 4.00m	4.00m to 4.25m	4.25m to 4.50m
Time per 0.5m (s)	**0.22**	**0.13**	**0.13**	**0.11**	**0.13**	**0.12**	**0.13**	**0.12**	**0.13**	**0.12**	**0.13**	**0.13**	**0.12**	**0.13**	**0.13**	**0.13**	**0.17**
Total elapsed time **per 0.25m**	**0.22**	**0.35**	**0.48**	**0.58**	**0.72**	**0.84**	**0.97**	**1.09**	**1.22**	**1.34**	**1.47**	**1.60**	**1.72**	**1.85**	**1.98**	**2.11**	**2.24**
Velocity (ms^{-1}) **per 0.25m**	**1.14**	**1.89**	**1.96**	**2.24**	**1.97**	**2.01**	**1.89**	**2.05**	**1.87**	**2.01**	**1.88**	**1.91**	**2.13**	**1.98**	**1.94**	**1.88**	**1.49**
Acceleration (ms^{-2}) **per 0,25m**	**5.18**	**5.77**	**0.50**	**2.57**	**-2.10**	**0.38**	**1.34**	**-1.37**	**1.16**	**-1.01**	**0.23**	**1.82**	**-1.23**	**0.11**	**-0.34**	**-0.41**	**-2.33**

Appendix 3. Average lateral acceleration of *D. obovata* diaspores from a state of rest to attainment of the horizontal wind speed where wind speed is highlighted in magenta and time increments in blue.

	Time increments (0.2s) and corresponding increase in diaspore lateral velocity (ms^{-1})																	
Wind speed	**0.02s**	**0.04s**	**0.06s**	**0.08s**	**0.10s**	**0.12s**	**0.14s**	**0.16s**	**0.18s**	**0.20s**	**0.22s**	**0.24s**	**0.26s**	**0.28s**	**0.30s**	**0.32s**	**0.34s**	**0.36s**
3kmhr^{-1} = 0.833 ms^{-1}	**0.05**	**0.098**	**0.147**	**0.197**	**0.246**	**0.295**	**0.344**	**0.393**	**0.442**	**0.491**	**0.540**	**0.590**	**0.639**	**0.688**	**0.737**	**0.786**	**0.835**	**0.884**
9kmhr^{-1} = 2.500 ms^{-1}	**0.15**	**0.295**	**0442**	**0.590**	**0.737**	**0.885**	**1.032**	**1.179**	**1.327**	**1.474**	**1.622**	**1.769**	**1.917**	**2.064**	**2.212**	**2.359**	**2.506**	**2.654**
15kmhr^{-1} = 4.17 ms^{-1}	**0.25**	**0.492**	**0.738**	**0.984**	**1.230**	**1.476**	**1.721**	**1.967**	**2.213**	**2.459**	**2.705**	**2.951**	**3.197**	**3.443**	**3.689**	**3.935**	**4.181**	**4.427**
21kmhr^{-1} = 5.83 ms^{-1}	**0.34**	**0.688**	**1.031**	**1.375**	**1.719**	**2.063**	**2.407**	**2.751**	**3.094**	**3.438**	**3.782**	**4.126**	**4.470**	**4.183**	**5.157**	**5.501**	**5.845**	**6.189**
27kmhr^{-1} = 7.50 ms^{-1}	**0.44**	**0.885**	**1.327**	**1.769**	**2.212**	**2.654**	**3.096**	**3.538**	**3.981**	**4.423**	**4.865**	**5.308**	**5.750**	**6.192**	**6.635**	**7.077**	**7.519**	**7.961**
33kmhr^{-1} = 9.17 ms^{-1}	**0.54**	**1.082**	**1.622**	**2.163**	**2.704**	**3.245**	**3.245**	**4.326**	**4.867**	**5.408**	**5.949**	**6.489**	**7.030**	**7.571**	**8.112**	**8.653**	**9.193**	**9.734**
39kmhr^{-1} = 10.83 ms^{-1}	**0.64**	**1.277**	**1.916**	**2.556**	**3.193**	**3.832**	**4.471**	**5.109**	**5.748**	**6.387**	**7.026**	**7.664**	**8.303**	**8.942**	**9.580**	**10.219**	**10.858**	**11.496**
45kmhr^{-1} = 12.50 ms^{-1}	**0.74**	**1.474**	**2.212**	**2.949**	**3.686**	**4.423**	**5.160**	**5.897**	**6.635**	**7.372**	**8.109**	**8.846**	**9.583**	**10.320**	**11.058**	**11.795**	**12.532**	**13.269**
51kmhr^{-1} = 14.17 ms^{-1}	**0.83**	**1.671**	**2.507**	**3.343**	**4.178**	**5.014**	**5.850**	**6.685**	**7.521**	**8.357**	**9.192**	**10.028**	**10.864**	**11.699**	**12.535**	**13.371**	**14.206**	**15.042**
57kmhr^{-1} = 15.83 ms^{-1}	**0.93**	**1.867**	**2.801**	**3.734**	**4.668**	**5.601**	**6.535**	**7.468**	**8.402**	**9.336**	**10.269**	**11.203**	**12.136**	**13.070**	**14.003**	**14.937**	**15.870**	**16.804**

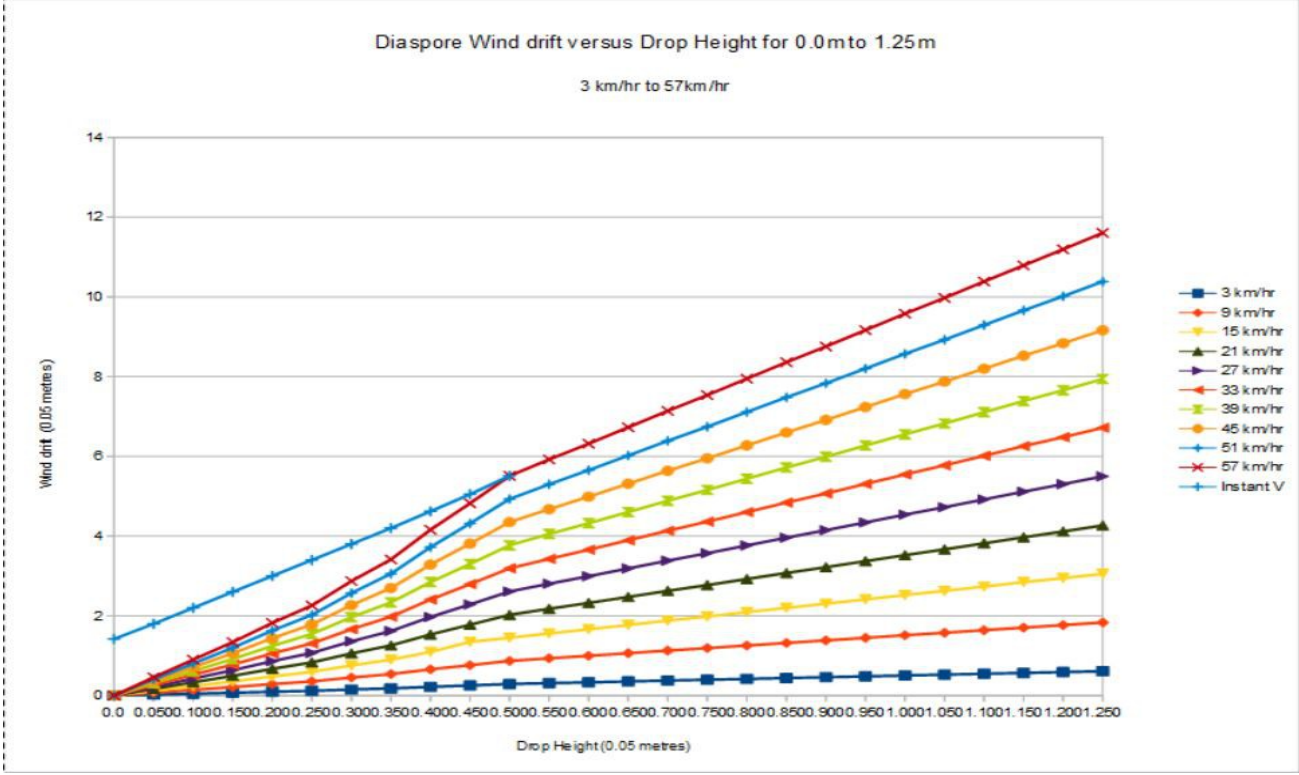
Appendix 4. Corrected average horizontal displacement of diaspores for the first 3.5m of drop height to account for the average time required to attain terminal velocity and wind speed.

[redacted]		Wind speed ms^{-1}																			
Drop Height	Fall time	0.83	1.67	2.50	3.33	4.17	5.00	5.83	6.67	7.50	8.33	9.17	10.00	10.83	11.67	12.50	13.33	14.17	15.00	15.83	16.67
1.25	0.73	0.61	1.22	1.83	2.43	3.05	3.67	4.27	4.89	5.50	6.11	6.72	7.33	7.94	8.55	9.16	9.77	10.38	11.00	11.61	12.22
1.20	0.71	0.59	1.18	1.77	2.36	2.95	3.54	4.12	4.71	5.30	5.89	6.48	7.07	7.66	8.25	8.84	9.43	10.02	10.61	11.19	11.79
1.15	0.68	0.57	1.14	1.70	2.27	2.84	3.41	3.97	4.55	5.12	5.68	6.25	6.82	7.39	7.96	8.53	9.09	9.66	10.23	10.80	11.37
1.10	0.66	0.55	1.09	1.64	2.19	2.73	3.28	3.82	4.37	4.92	5.47	6.01	6.56	7.11	7.65	8.20	8075	9.29	9.84	10.39	10.94
1.05	0.63	0.53	1.05	1.58	2.10	2.63	3.15	3.67	4.20	4.73	5.25	5.78	6.30	6.83	7.35	7.88	8.40	8.93	4.45	9.98	10.50
1.00	0.59	0.49	0.98	1.48	1.97	2.46	2.95	3.44	3.93	4.43	4.92	5.41	5.90	6.39	6.88	7.38	7.87	8.84	8.85	9.34	10.84
0.95	0.58	0.48	0.97	1.45	1.93	2.41	2.90	3.37	3.86	4.34	4.83	5.31	5.79	6.27	6.76	7.24	7.72	8.20	8.65	9.17	9.65
0.90	0.56	0.46	0.92	1.38	1.84	2.30	2.77	3.22	3.69	4.15	4.61	5.07	5.53	5.99	6.45	6.91	7.37	7.83	8.30	8.76	9.22
0.85	0.53	0.44	0.88	1.32	1.76	2.20	2.64	3.07	3.52	3.96	4.40	4.84	5.28	5.72	6.16	6.60	7.04	7.48	7.920	8.36	8.80
08.0	0.50	0.42	0.84	1.26	1.67	2.09	2.51	2.92	3.35	3.77	4.18	4.60	5.02	5.44	5.86	6.28	6.69	7.11	7.53	7.95	8.37
0.75	0.48	0.40	0.80	1.19	1.59	1.96	2.38	2.77	3.17	3.57	3.97	4.36	4.76	5.16	5.55	5.95	6.35	6.74	7.14	7.54	7.94
0.70	0.45	0.38	0.75	1.13	1.50	1.88	2.26	2.63	3.01	3.38	3.76	4.13	4.51	4.89	5.26	5.64	6.01	6.40	6.77	7.14	7.52
0.65	0.43	0.35	0.71	1.06	1.42	1.77	2.13	2.47	2.833	3.17	3.54	3.90	4.25	4.60	4.96	5.31	5.67	6.02	6.38	6.73	7.09
0.60	0.40	0.33	0.67	1.00	1.33	1.66	2.00	2.32	2.66	2.99	3.33	3.66	3.99	4.32	4.66	4.99	5.32	5.65	5.99	6.32	6.65
0.55	0.37	0.31	0.62	0.94	1.25	1.56	1.87	2.18	2.49	2.81	3.12	3.43	3.74	4.05	4.36	4.68	4.99	5.30	5.61	5.92	6.24
0.50	0.35	0.29	0.58	0.87	1.16	1.45	1.74	2.03	2.32	2.61	2.90	3.19	3.48	3.77	4.06	4.35	4.64	4.93	5.22	5.51	5.80
0.45	0.32	0.25	0.51	0.76	1.02	1.35	1.52	1.78	2.03	2.27	2.54	2.80	3.04	3.30	3.56	3.81	4.06	4.32	4.57	4.82	5.08
0.40	0.30	0.22	0.44	0.66	0.88	1.10	1.31	1.53	1.75	1.97	2.19	2.41	2.63	2.85	3.07	3.28	3.50	3.72	3.94	4.16	4.3
0.35	0.27	0.18	0.37	0.54	0.72	0.90	1.08	1.23	1.44	1.62	1.80	1.98	2.16	2.34	2.52	2.70	2.88	3.06	3.24	3.42	3.60
0.300	0.25	0.15	0.30	0.45	0.60	0.76	0.91	1.06	1.21	1.36	1.51	1.67	1.81	1.96	2.12	2.27	2.42	2.57	2.72	2.87	3.02
0.25	0.22	0.12	0.24	0.36	0.48	0.60	0.71	0.83	0.95	1.07	1.19	1.31	1043	1.55	1.67	1.78	1.90	2.02	2.14	2.26	2.38
0.20	0.20	0.10	0.16	0.29	0.38	0.48	0.58	0.67	0.77	0.86	0.96	1.06	1.15	1.25	1.34	1.44	1.53	1.63	1.73	1.82	1.92
0.15	0.17	0.07	0.14	0.21	0.28	0.35	0.42	0.49	0.57	0.64	0.71	0.78	0.85	0.92	0.99	1.06	1.13	1.20	1.27	1.34	1.41
0.10	0.14	0.05	0.10	0.14	0.19	0.24	0.29	0.33	0.38	0.43	0.48	0.52	0.58	0.62	0.67	0.71	0.76	0.81	0.85	0.90	0.95
0.05	0.10	0.02	0.05	0.07	0.10	0.12	0.14	0.17	0.19	0.22	0.24	0.27	0.29	0.31	0.33	0.36	0.39	0.41	0.43	0.46	0.48
0.00	0.00	0.00	0.00	0.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Drop height	Fall time	3.00	6.00	9.00	12.00	15.00	18.00	21.00	24.00	27.00	30.00	33.00	36.00	39.00	42.00	45.00	48.00	51.00	54.00	57.00	60.00
[redacted]		Wind speed $km.hr^{-1}$																			

Appendix 5. Average horizontal displacement of diaspores (m) at 0.5m increments in vertical height for the drop heights of 0.0m – 10.0m in response to increasing wind strengths.

[redacted]		Wind speed ms^{-1}																			
Drop Height	**Fall time**	**0.83**	**1.68**	**2.50**	**3.33**	**4.17**	**5.00**	**5.83**	**6.67**	**7.50**	**8.33**	**9.17**	**10.00**	**10.83**	**11.67**	**12.50**	**13.33**	**14.17**	**15.00**	**15.83**	**16.68**
10.00	**5.18**	4.32	8.64	12.96	17.27	21.59	25.91	30.23	34.55	38.87	43.18	47.50	51.82	56.14	60.46	64.78	69.09	73.41	77.73	82.05	86.38
9.50	**4.87**	4.056	8.12	12.18	16.24	20.30	24.36	28.41	32.48	36.54	40.60	44.66	48.72	52.78	56.84	60.90	64.96	69.02	73.08	77.14	81.22
9.00	**461**	3.84	7.69	11.54	15.4	19.23	23.08	26.92	30.77	34.61	38.46	42.31	46.15	49.99	53.84	57.69	61.53	65.38	69.23	73.07	76.93
8.50	**4.35**	3.63	7.27	10.90	14.53	18.16	21.80	25.43	29.06	32.69	36.32	39.96	43.59	47.22	50.86	54.49	58.12	61.75	65.39	69.02	72.67
8.00	**4.10**	3.42	6.84	10.26	13.68	17.10	20.52	23.93	27.36	30.77	34.19	37.61	41.03	44.45	47.87	51.29	54.71	58.13	61.55	64.96	68.40
7.50	**3.84**	3.20	6.41	9.62	12.82	16.03	19.23	22.43	25.64	28.85	32.05	35.26	38.46	41.66	44.87	48.08	51.28	54.49	57.69	60.89	64.11
7.00	**3.59**	2.99	5.99	8.98	11.96	14.96	17.95	20.84	23.94	26.93	29.92	32.91	35.90	38.89	41.89	44.88	47.87	50.86	53.85	56.84	59.85
6.50	**3.33**	2.78	5.56	8.33	11.11	13.89	16.67	19.44	22.22	25.00	27.77	30.55	33.33	36.11	38.88	41.66	44.44	47.22	50.00	52.77	55.56
6.00	**3.07**	2.56	5.13	7.69	10.26	12.82	15.39	17.95	20.51	23.08	25.64	28.21	30.77	33.33	35.90	38.90	41.03	43.59	46.16	48.72	51.29
5.50	**2.82**	2.35	4.70	7.05	9.40	11.76	14.11	16.46	18.81	21.16	23.51	25.86	28.21	30.56	32.91	35.26	37.61	39.97	42.32	44.67	47.03
5.00	**2.56**	2.14	4.27	6.41	8.55	10.68	12.82	14.96	17.09	19.23	21.37	23.50	25.64	27.78	29.91	32.05	34.19	36.32	38.46	40.60	42.74
4.50	**2.41**	2.01	4.02	6.03	8.03	10.04	12.05	14.06	16.07	18.08	20.08	22.09	24.10	26.11	28.12	30.13	32.13	34.14	36.15	38.16	40.18
4.00	**2.11**	1.76	3.52	5.28	7.03	8.79	10.55	12.31	14.07	15.83	17.58	19.34	21.10	22.86	24.61	26.38	28.13	29.90	31.65	33.41	35.17
3.50	**1.85**	1.54	3.08	4.63	6.17	7.71	9.25	10.79	12.33	13.88	15.42	16.96	18.50	20.04	21.58	23.13	24.67	26.21	27.75	29.29	30.84
3.00	**1.60**	1.33	2.67	4.00	5.33	6.67	8.00	9.33	10.67	12.00	13.33	14.67	16.00	17.33	18.67	20.00	21.33	22.67	24.00	25.33	26.67
2.50	**1.34**	1.12	2.23	3.35	4.47	5.58	6.70	7.82	8.93	10.05	11.17	12.28	13.40	14.52	15.63	16.75	17.87	18.98	20.10	21.22	22.34
2.00	**1.09**	0.91	1.82	2.73	3.63	4.54	5.45	6.36	7.27	8.18	9.08	9.99	10.90	11.81	12.72	13.62	14.53	15.44	16.3	17.26	18.17
1.50	**0.84**	0.70	1.40	2.10	2.80	3.50	4.20	4.90	5.60	6.30	7.00	7.70	8.40	9.10	9.80	10.50	11.20	11.90	12.60	13.30	14.00
1.00	**0.59**	0.49	0.98	1.48	1.97	2.46	2.95	3.44	3.93	4.43	4.92	5.41	5.90	6.39	6.88	7.38	7.87	8.8.36	8.85	9.34	10.84
0.50	**0.34**	0.29	0.58	0.87	1.16	1.45	1.74	2.03	2.32	2.61	2.90	3.19	3.48	3.77	4.06	4.35	4.64	4.93	5.22	5.51	5.80
0.00	**0.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Drop height	**Fall time**	**3.0**	**6.0**	**9.0**	**12.0**	**15.0**	**18.0**	**21.0**	**24.0**	**27.0**	**30.0**	**33.0**	**36.0**	**39.0**	**42.0**	**45.0**	**48.0**	**51.0**	**54.0**	**57.0**	**60.0**
[redacted]		Wind speed $km.hr^{-1}$																			

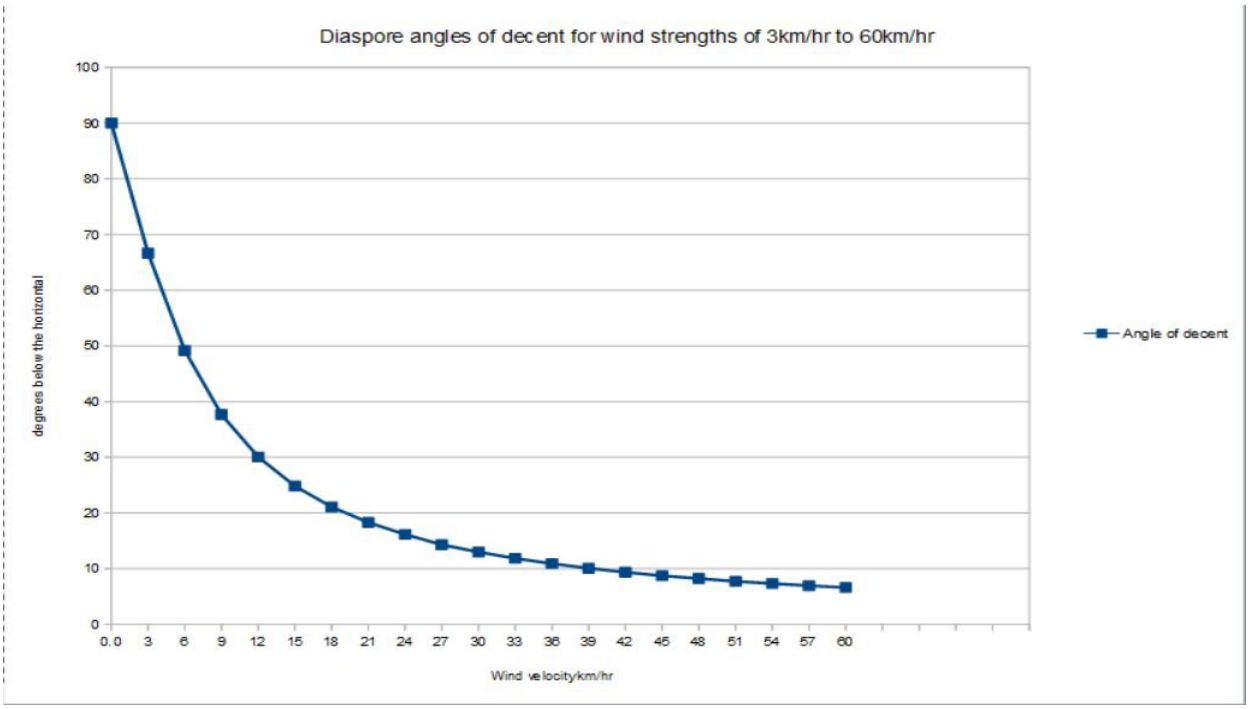
Appendix 6. Average horizontal wind drift of *D. obovata* diaspores under varying combinations of release height and wind velocity with the effect of assumption of instantaneous velocity displayed for a wind velocity of 57km hr^{-1}.



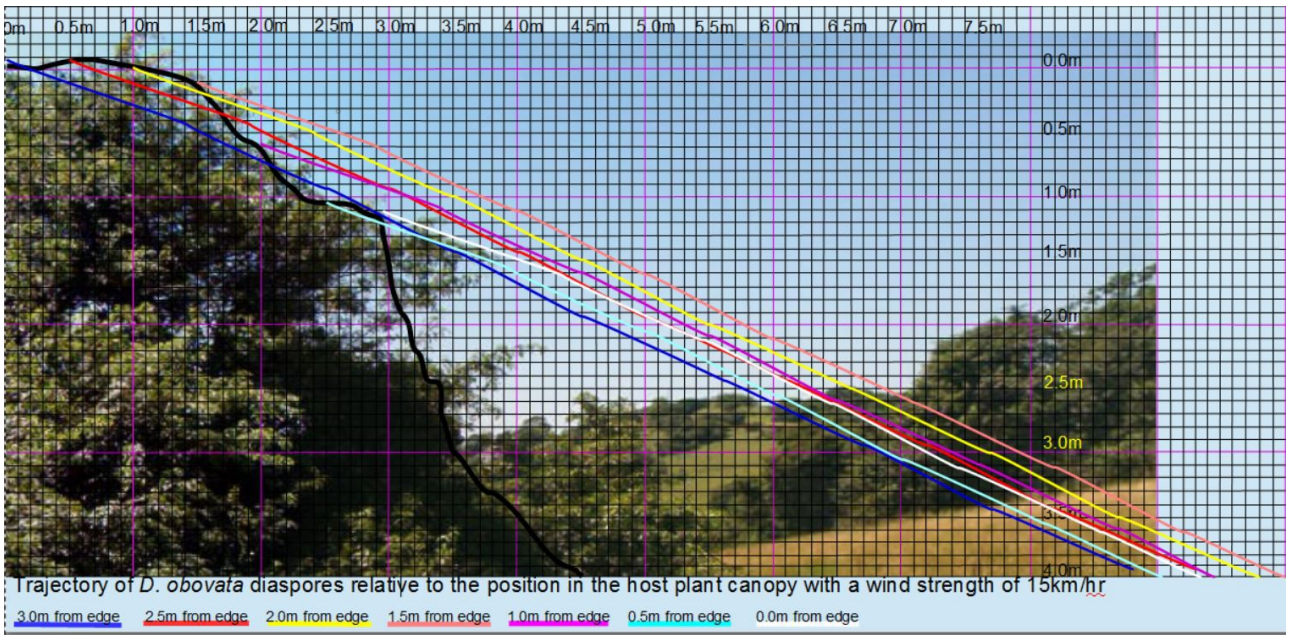
Appendix 7. Angle of decent of *D. obovata* diaspores below the horizontal plane in relation to wind strength and corresponding canopy gradients where the angle of decent = tan^{-1} x (drop height / wind displacement).

Wind speed Km hr^{-1}	**3.00**	**6.00**	**9.00**	**12.00**	**15.00**	**18.00**	**21.00**	**24.0**	**27.00**	**30.00**
Wind speed ms^{-1}	**0.83**	**1.67**	**2.50**	**3.33**	**4.177**	**5.00**	**5.83**	**6.67**	**7.50**	**8.33**
Angle of decent below horizontal	**66.64°**	**49.16°**	**37.67°**	**30.07°**	**24.84°**	**21.10°**	**18.31°**	**16.17°**	**14.31°**	**13.01°**
Wind speed Km hr^{-1}	**33.00**	**36.00**	**39.00**	**42.00**	**45.00**	**48.00**	**51.00**	**54.00**	**57.00**	**60.00**
Wind speed ms^{-1}	**9.17**	**10.00**	**10.83**	**11.67**	**12.50**	**13.33**	**14.17**	**15.00**	**15.83**	**16.67**
Angle of decent below horizontal	**11.86°**	**10.92°**	**10.09°**	**9.38°**	**8.75°**	**8.25°**	**7.74°**	**7.35°**	**6.96°**	**6.62°**

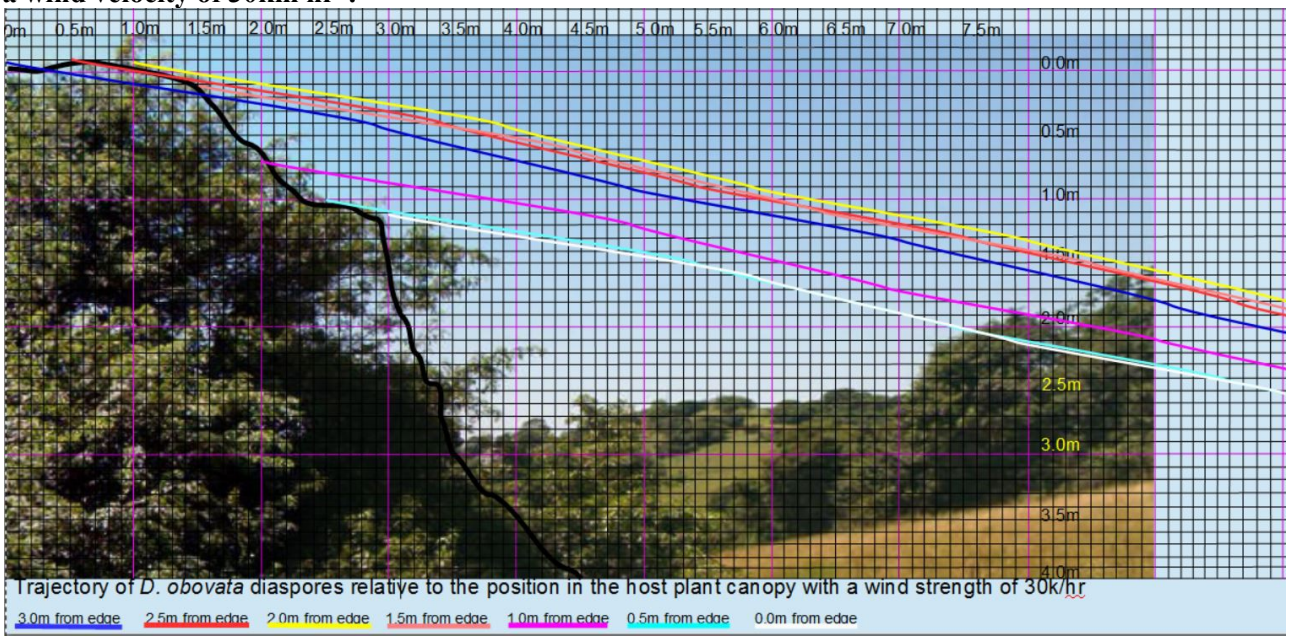
Appendix 8. Diaspore angles of decent below the horizontal for varying wind strengths



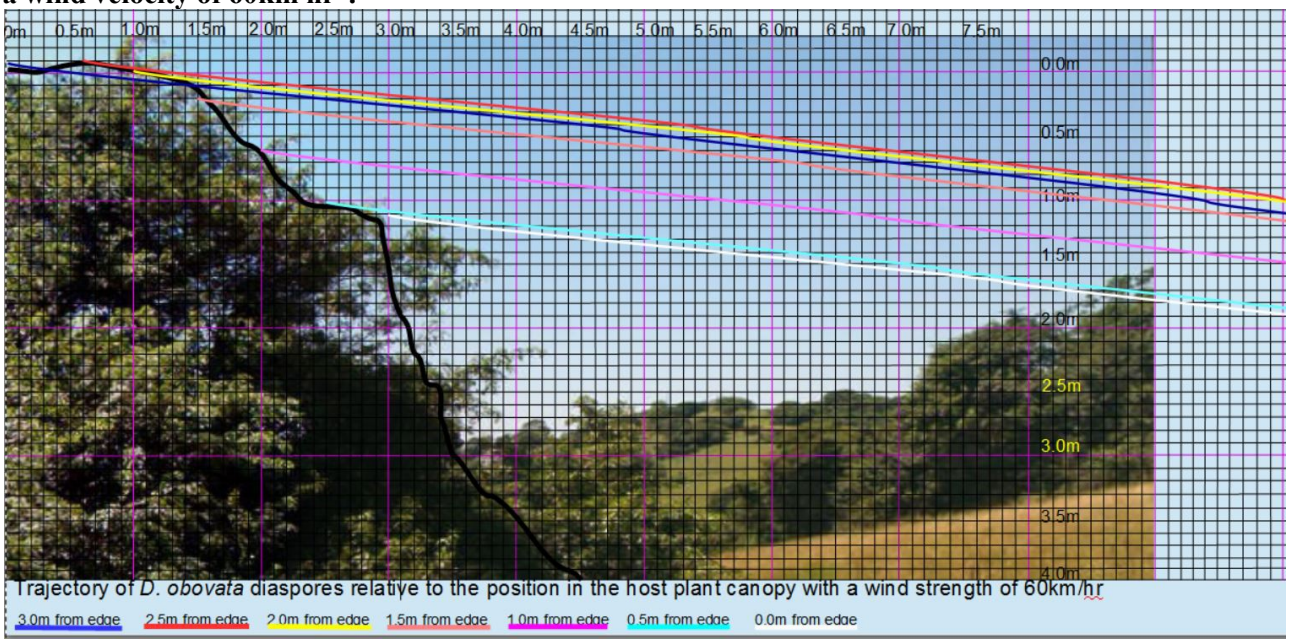
Appendix 9. Diaspore angle of decent superimposed over a generic canopy profile (as indicated by the black line) and the required distance from the edge of the canopy to clear the edge of the host tree, for a wind velocity of 15km hr^{-1}.



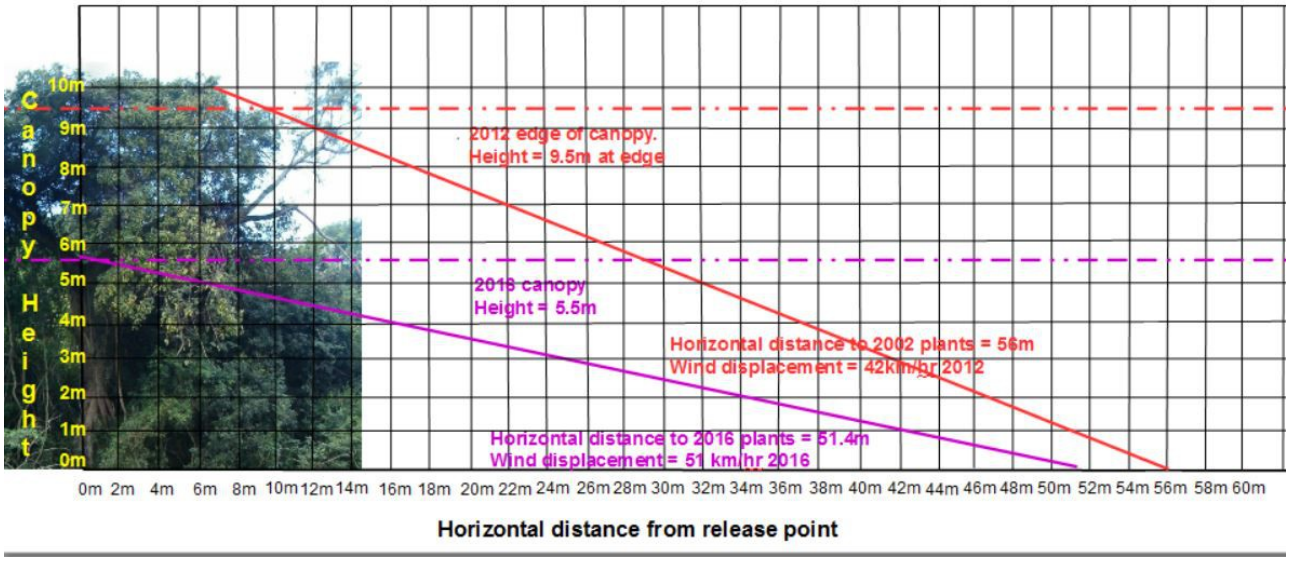
Appendix 10. Diaspore angle of decent superimposed over a generic canopy profile (as indicated by the black line) and the required distance from the edge of the canopy to clear the edge of the host tree, for a wind velocity of 30km hr^{-1}.



Appendix 11. Diaspore angle of decent superimposed over a generic canopy profile (as indicated by the black line) and the required distance from the edge of the canopy to clear the edge of the host tree, for a wind velocity of 60km hr^{-1}.

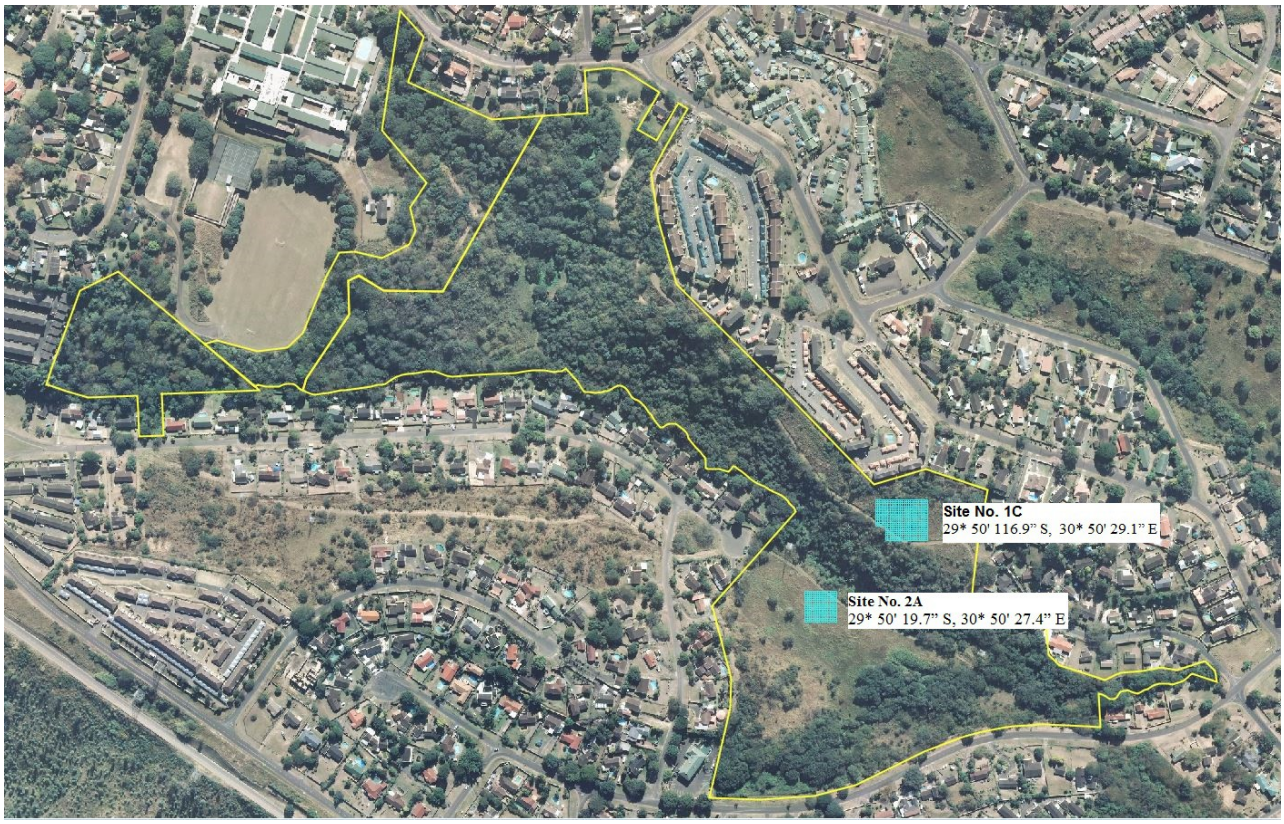


Appendix 12. Vertical heights of D. obovata in the host tree at survey area 2A at Marian Wood Nature Reserve before and after the 2012 storm event and the altered horizontal distance of stands of *D. obovata* mapped in the grassland in relation to the parent plant with the angles of decent and associated wind velocities derived from appendix 5.

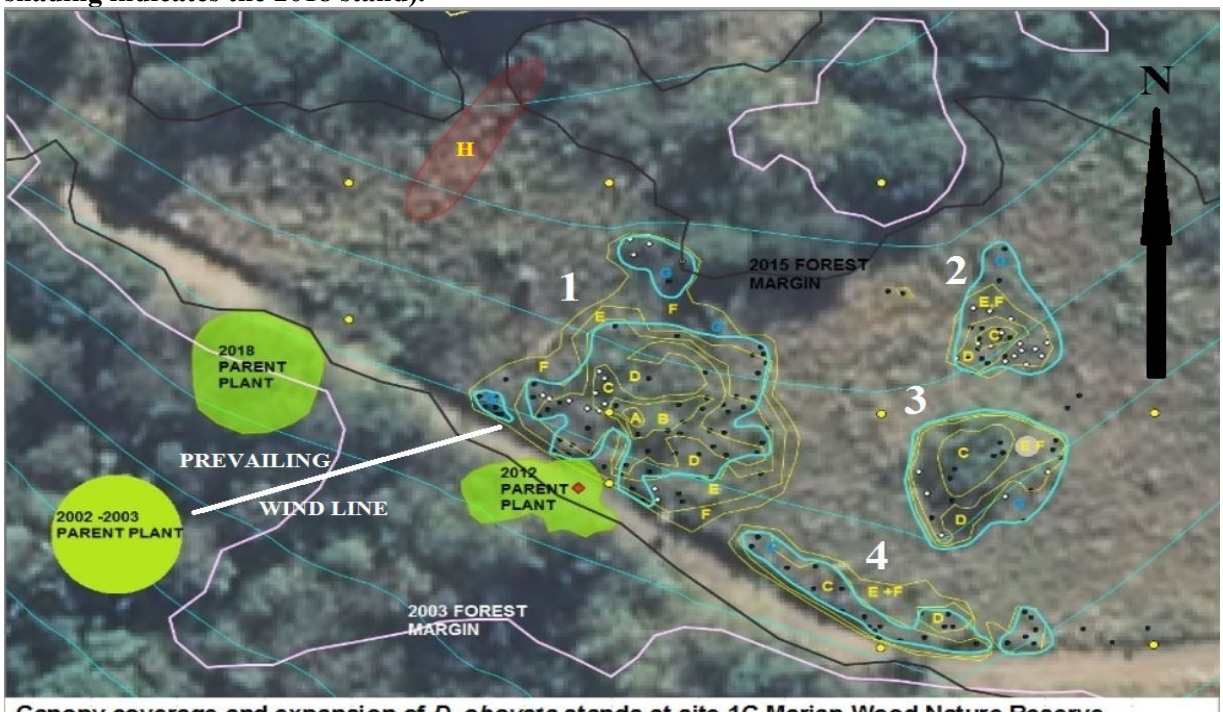


Appendix 13. Unidentified species of termite recorded harvesting D. obovata diaspores from baskets at Marian Wood Nature Reserve.

Appendix 14. Survey sites, Marian Wood nature Reserve, Pinetown, eThekwini Municipality. (29° 50' 18.50'' S, 30° 50' 29.20” E)

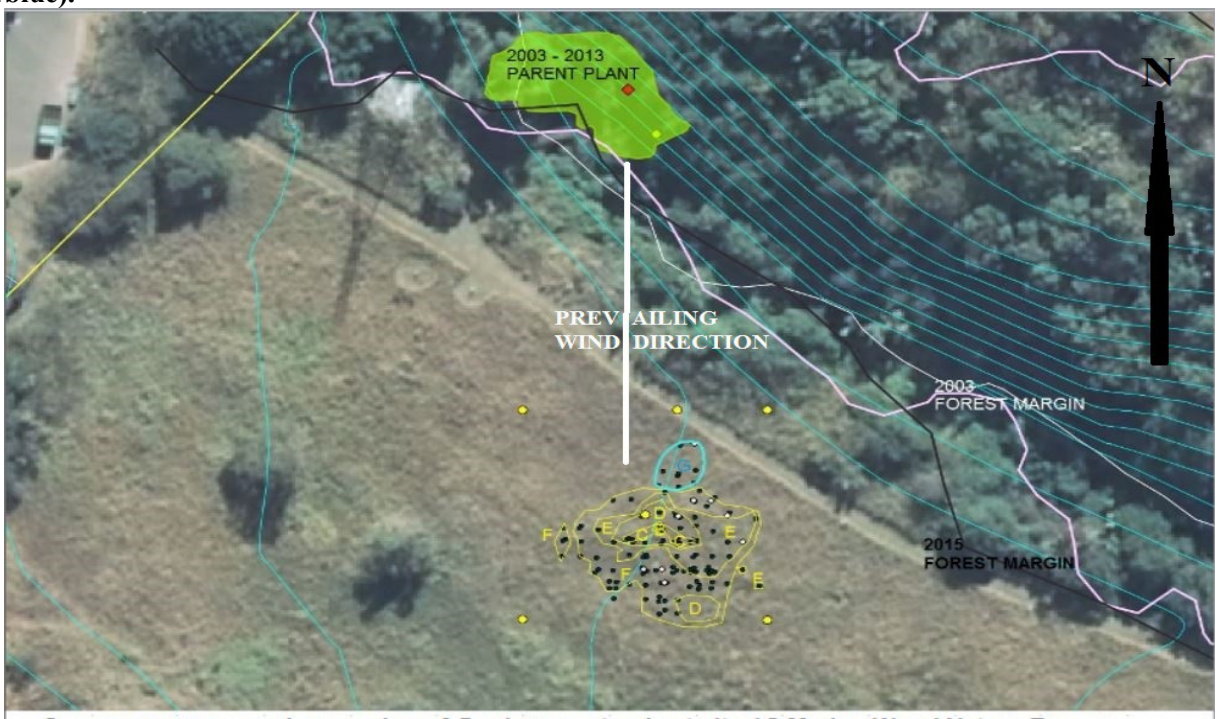


Appendix 15. Mapping of the establishment and expansion of stands of *D. obovata* at site 1C, Marian Wood Nature Reserve, (Where yellow dots indicate survey posts. Black and white dots show the positions of individual plants. Expansion and contraction of stands indicated in yellow and blue. Red shading indicates the 2018 stand).



Canopy coverage and expansion of *D. obovata* stands at site 1C Marian Wood Nature Reserve from from 1999/2000 – 2015 against the 2015 backdrop layer where A = 1999, B = 2003, C = 2006, D = 2008, E = 2010, F = 2012, G = 2015 and H = 2018

Appendix 16. Mapping of the establishment and expansion of stands of *D. obovata* at site 2A, Marian Wood Nature Reserve, (Where yellow dots indicate survey posts. Black and white dots show the positions of individual plants and the expansion and break up of stands is indicated in yellow and blue).



Canopy coverage and expansion of *D. obovata* stands at site 1C Marian Wood Nature Reserve from from 1999/2000 – 2015 against the 2015 backdrop layer where A = 1999, B = 2003, C = 2006, D = 2008, E = 2010, F = 2012 and G = 2015 areas of encroachment.

Appendix 17. Establishment of *D obovata* stands in Marian Wood grasslands relative to the adjacent forest, recorded canopy heights and corresponding calculated wind strengths required for effective diaspore dispersal into the grasslands as per comparison of mapped plants with the GIS data.

Survey site	Year	Plant Number	Distance from canopy / host tree	Height of canopy / host tree	Height above the stand	Corresponding wind strength required for diaspore dispersal
1C	2002	1C1	22.2m	≤ 8.0m	≤ 4.0m	37km/hr
2A	2003	2A1	56.0m	≤ 9.5m	≤ 9.5m	42km/hr
1C	2006	1C2	35.0m	≤ 7.0m	≤ 5.0m	51km/hr
1C	2006	1C3	21m	≤ 7.0m	≤ 5.0m	30km/hr
1C	2006	1C4	5.1m	≤ 7.0m	≤ 5.0m	9km/hr
2A	2008	2A2	64.5m	≥ 9.5m	≥ 9.5m	42km/hr
2A	2015	2A3	51.0m	5.5m	5.5m	51km/hr
1C	02/2018	1C5	13.0m to 28.5m	6.5m	+3.5m to – 0.5m	24km hr^{-1} to 92km hr^{-1}
Wind speeds at Marian Wood NR on the 17th October 2017 measured with a Kestrel hand held anemometer serial No. 2278445 reached 89km hr^{-1}						
Survey site	Predominant wind directions					
1C	North East and South West					
2A	North and South					

Appendix 18. Expansion of *D. obovata* stands at Marian Wood Nature Reserve, 2002 – 2018 as identified by comparison of the mapped positions of individual ramets and seedlings at sites 1C and 2A against the available historical orthophotos.

Year	Site /stand	width	length	Area	Expansion	comments
1999	1C					No record of *D. obovata* in survey site. Annual burn in 1999, 2000, 2001
2002	1C	1.64m	1.69m	1.67m^2	1.67m^2	1st record of *D. obovata* in grassland, not visible on ortho photo.
2003	1C / 1	7.78m	3.78m	14.26m^2	12.59m^2 = +753.89%	No burn in 2002
	1C / 2					not visible on ortho photo.
	1C / 3					not visible on ortho photo.
	1C / 4					not visible on ortho photo.
2006	1C / 1	12.60m	11.44m	57.19m^2	42.93m^2 = +301.05%	annual burn 2006
	1C / 2	3.08m	1.90m	3.98m^2	3.98m^2	
	1C / 3	5.63m	6.14m	23.42m^2	23.42m^2	
	1C / 4	20.64m	3.34m	46.08m^2	46.08m^2	
2008	1C / 1	17.34m	14.10m	150.22m^2	93.03m^2 = +162.67 %	annual burn 2008
	1C / 2	5.57m	4.47m	14.46m^2	10.48m^2 = +263.32%	
	1C / 3	11.26m	11.65m	83.26m^2	59.84m^2 = +255%	
	1C / 4	20.64m	4.94m	50.59m^2	4.51m^2 = +9.79%	
2010	1C / 1	19.77m	17.69m	229.60m^2	79.38m^2 = +52.84%	No burns from 2009 - 2011
stand 2	1C / 2	8.21m	7.80m	39.98m^2	25.52m^2 = +176.49%	
stand 3	1C / 3	10.88m	11.03m	63.65m^2	-19.16m^2 = -23.55 %	Stand has contracted from 2008 area.
stand 4	1C / 4	21.47m	6.65m	89.11m^2	38.52m^2 = +76.14%	
2012 stand 1	1C / 1	24.16m	25.82m	339.85m^2	110m^2 = +48.01%	Cut stump treatment of entire site 1C with 5% amazaphir and annual grassland burns in 2013. Parent plant cut and treated with 5% picloram
stand 2	1C / 2	8.21m	7.80m	39.98m^2	0.0m^2 = 0.0%	No change from 2010
stand 3	1C / 3	10.88m	11.03m	63.65m^2	0.0m^2 = 0.0%	No change from 2010
stand 4	1C / 4	25.19m	6.65m	102.27m^2	13.16m^2 = +14.77%	No expansion of original stand from 2010 but addition of second, new stand in 2012.
2015	1C / 1	2.61m 5.59m 18.07m	2.68m 5.31m 15.95m	4.51m^2 18.54m^2 176.47m^2	Total = 199.52m^2 = - 58.71%	Cut stump treatment of all plants in site 1C with 5% amazaphir in May and annual burn in September. Visible canopy area has reduced in area and broken into three groups
	1C / 2	8.12m	11.92m	59.18m^2	18.20m^2 = +45%	
	1C / 3	11.80m	12.12m	105.45m^2	41.8m^2 = +65.67%	
	1C / 4	21.06m 4.04m	3.82m 4.31m	45.11m^2 10.30m^2	Total = - 46.86m^2 = - 45.82%	Stand 4 has broken into 2 separate smaller stands
2018	1C /5	3.80m	16.20m	50.0m^2		New stand of scattered seedling sand a new parent plant identified in 02/2018. Seedlings and parent plant surveyed and mapped after grassland burns in 09/2018.
Year		width	length	Area	Expansion	comments
1999	2A					No record of *D. obovata* in grassland. Nothing visible on ortho photo.
2002	2A					No record of *D. obovata* in grassland. Nothing visible on ortho photo.
2003	2A	1.30m	1.21m	0.87m^2	0.87m^2	Five plants visible in rough rosette. Annual burns in 2003m and 2005
2006	2A	8.90m > 7.6	3.30m	11.01m^2	10.14m^2 = 1165.52%	
2008	2A	10.87m > 1.97 5.42m	7.00m 3.8m	46.75m^2 16.02m^2	51.76m^2 = 470.12%	New stand visible. Burns done in 2007 + 2009
2010	2A	19.85m > 8.98 5.42m	11.80m 3.8m	128.05m^2 16.02m^2	81.30m^2 = 129.52%	No visible increase on second stand. No burning done in 2010 or 2011.
2012	2A	25.13m > 5.28	19.69m	319.79m^2	175.72m^2 = 121.97%	Individual clusters have joined. New smaller plants visible on edges of stand. Cut stump treatment with 5% picloram and successive annual burn.
2013	2A	No surviving individual's recorded from 2012 survey that were treated with 5% picloram. Host tree of source parent was broken in a storm, March 2012.				
2015	2A	Nine new seedlings recorded in June 2015 and treated with 5% picloram. Source parent plant cut and treated with 5% picloram in June 2015.				
2018	2A	No New seedlings recorded from 11/2015 – 09/2018.				

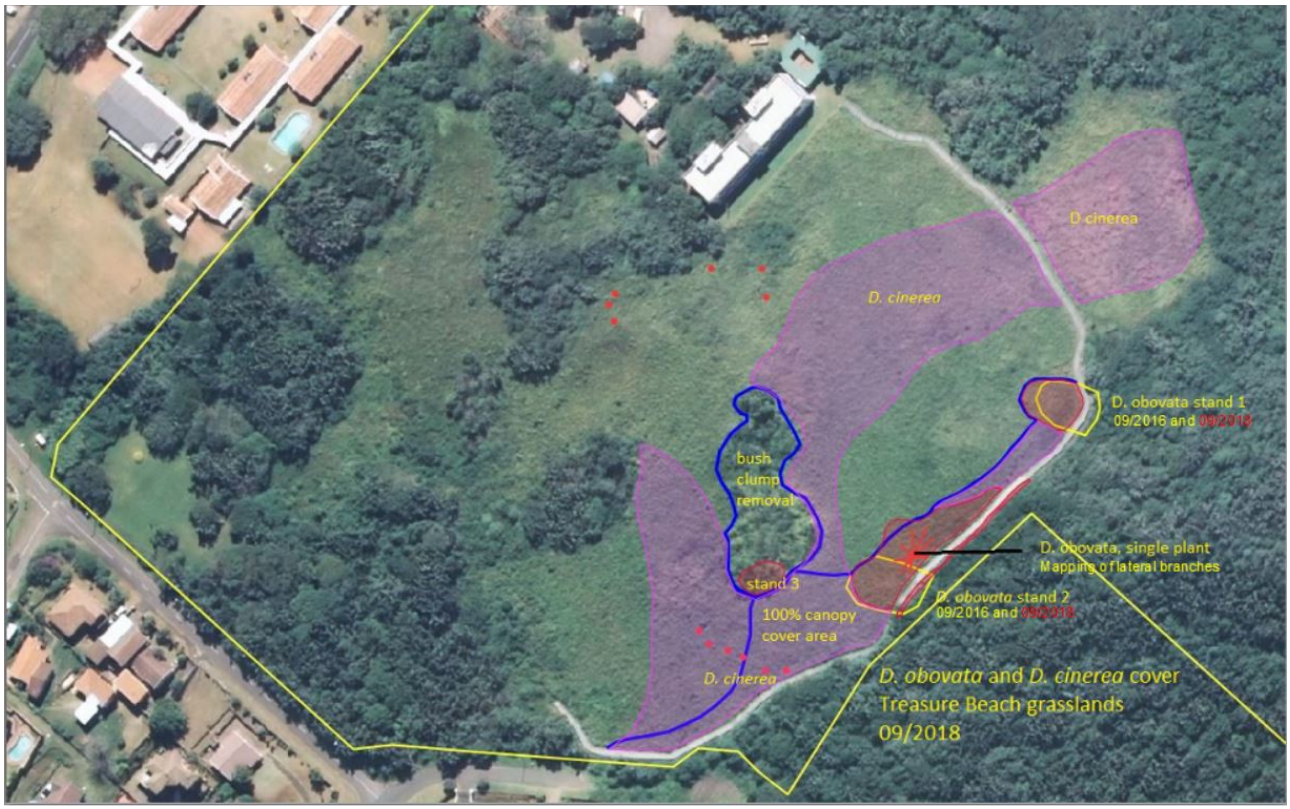
Appendix 19. Clonal root mapping, site 1C, Marian Wood Nature Reserve (Where magenta lines show the roots and the expansion and contraction of stands is indicated in yellow and white.

Appendix 20. Exposure of clonal root network, site 1C, plant No 1, Marian Wood Nature Reserve

Appendix 21. Mapping of the spread of *D. obovata* and *D. cinerea* over a two year period and the lateral branches of a particular *D. obovata* at Treasure Beach Grasslands Reserve

Original grassland cover (2003 ortho photos) and net gains or losses (2016 ortho photos) as compared to field surveys September 2018				
	2016 extent	2018 extent		% change
Grassland cover	27743m^2 (approx)	26601m^2 (approx)	- 1142m^2 (approx)	4% net loss
Dalbergia obovata stand 1	139m^2	208m^2	+ 69m^2	49.6%
Dalbergia obovata stand 2	220m^2	530m^2	+ 310m^2	140%
Dalbergia obovata stand 3	0.0m^2	93m^2	+ 93m^2	
Dalbergia obovata stand 2 – clonal plant		132m^2		25% of stand
Dichrostachys cinerea	Not recorded	8830m^2	+ 8830m^2	
Bush clump removal		1193m^2		
Extent of 100% canopy cover by *D. obovata* and *D. cineria.*	Not recorded	2335m^2		
Remaining area of grassland encroached to some extent by D. cinera		6495m^2		
Total area of current grassland encroached by *D. obovata* and *D. cinerea*	359m^2	9661m^2		2691.09% increase
Lengths of the lateral branches of the stand 2 - clonal plant. Clockwise starting from North	Branch 1 branch 2 branch 3 branch 4 branch 5 branch 6 branch 7 branch 8 branch 9 branch 10		6.0m 7.8m 10.1m 8.8m 6.9m 4.5m 4.3m 5.1m 6.2m 6.4m	

Appendix 22. September 2018 extent of encroachment of Treasure Beach grasslands by *D. obovata* and *D. cinerea*.



Appendix 23. Measurement of *D. obovata* lateral branches, Treasure Beach grasslands, (Where yellow circles indicate the tips of the lateral branches and the main central stem is indicated by a yellow star).

Appendix 24. *D. obovata* rooting of lateral branches, Treasure Beach grasslands, (Indicated by yellow circles).

Chapter 4: Discussion and conclusions

4.1 Discussion

The encroachment of moist coast grasslands by *D. obovata* was identified as a threat to this habitat within the eThekwini Municipal area. Searches of available literature identified encroachment of grasslands by woody plant species (Chapter 1 and Chapter 2) as a worldwide phenomenon (Naito and Cairns, 2011). The primary driver associated with the global increase in bush encroachment was identified as the increase in atmospheric CO_2 (Wigley et al., 2009, Battipaglia et al., 2013) but that this was either moderated or aggravated at a local level by other factors such as mean annual precipitation (Devine et al., 2017), fire regimes (Higgins et al., 2000, Bock et al., 2007), the management of IAPs (Archer and Predick, 2014) and the presence or absence of large herbivores which may result in overgrazing (Ansley et al., 2006, Ward, 2010). It was noted that the woody plant species commonly cited in studies of bush encroachment were self-supporting trees or bushes and no records were found of encroachment of grasslands by lianas or climbing plants (De Kler, 2004. Bond and Midgley, 2012, Su et al., 2015).

Competition between grasses and seedlings of woody plants for resources has been cited as a limiting factor for the recruitment of seedlings into the adult tree populations in grasslands (Ward, 2010). Although *D. obovata* seedlings would have to compete directly with grasses for resources this is not the case for ramets produced produced from the lateral roots or the rooting of lateral branches of plants using clonal propagation of (Fahrig et al., 1994). The clonal propagation of *D. obovata* was confirmed by the mapping of plant roots and lateral branches of *D. obovata* stands (Chapter 3). New immature shoots are able to access the carbon and nutrient resources of the entire plant (Oborny et al., 2000) with its developed photosynthetic capacity and can therefore invest in vertical growth through the grass canopy. Once the shoots are clear of the grass canopy and are no longer shaded they are then able to add to the photosynthetic capacity of the entire physiologically integrated genet (Hartnett and Bazzaz, 1983). It has also been noted that C3 trees growing under conditions of elevated CO_2 are also able to increase the allocation of carbon storage to their roots (Curtis and Wang, 1998, Bond and Midgley, 2012), which allows for an increased availability of stored resources for the regeneration of photosynthetic capacity after fires and that, “Frequent surface fires in savannas select for woody plants with underground storage organs, or clonally spreading root systems, which

promote rapid post-burn recovery" (Bond and Midgley, 2012).

The resistance of *D. obovata* to fire was noted from the available reserve management records and that the stands mapped at Marian Wood Nature Reserve continued to expand following the implementation of controlled annual burns (Chapter 3). This was supported by the results of the Chi-sqare tests (Chapter 2) which confirmed that there is no relationship between fire regimes and *D. obovata* encroachment. The PCA did however confirm that there was also a weak correlation between the use of back fires versus head fires (Chapter 2). The use of back fires are associated with the depression of the post burn regrowth of grasses which compete with *D. obovata*, whereas head fires are associated with hotter burns which which results in a greater kill of woody vegetation top stems (Trollope and Trollope, 2010). Generally the results of the Chi-square tests and PCA showed that *D. obovata* was not effectively controlled through historic bush encroachment management practices. On the other hand it was noted in (Chapter 3) that at survey site 2A the application of 5% picloram as a cut stump treatment resulted in a 100% mortality of all treated plants. The presence of short stunted *D. obovata* plants on the edge of forests and bush clumps which conformed to the general description of Gulivers were recorded at New Germany Nature Reserve and Roosefontein Nature Reserve (Chapter 2). The ability of *D. obovata* to propagate clonally and the increased capacity for clonal C3 plants to store carbon reserves in their roots in the presence of increased atmospheric CO_2 would then also increase the rates of post burn recovery after fires and enable "Gullivers" to grow beyond the top kill zone, escape the fire trap and be recruited into the adult population (Battipaglia 2012,. Giradin etal 2016,).

The relationship between the absence of large herbivores in the grasslands and encroachment by *D. obovata* was confirmed by both the Chi-square tests and the PCA (Chapter 2). Exactly how large herbivores notably mixed feeders prevented *D. obovata* from encroaching into the grasslands where they were present is not understood. Whether or not the presence or absence of large herbivores was part of an active management strategy of the study areas, they were a component of the grassland ecosystem in which *D. obovata* was being studied. Similar relationships between mixed feeder herbivores, including impala, and the suppression or reduction of woody plant species in grasslands has been recorded globally (Roques et al., 2001, Maher et al., 2010, Su et al., 2015, Sankaran et al., 2013, Cornelissen et al., 2014). More recently the impact of mule deer on the recovery of clonally reproducing *Populus tremuloides* (Rogers and McAvoy, 2018) by over

browsing on adventitious shoots which suppressed the growth of new saplings has been reported. It is suggested that a similar relationship may exist between *D. obovata* and mixed feeders such as the domestic goats and impala recorded in the grasslands where *D. obovata* was absent, in that browsing on *D. obovata* seedlings may reduce their capacity to successfully compete with grasses for available resources and be recruited into the adult population. This relationship does however require further investigation.

There are key differences between the physiology and development of lianas and self supporting woody plants, the most significant of which is the lack of a self-supporting stem which requires the investment of carbon resources in the form of sclerenchyma and lignin. Lianas can therefore invest in the production of secondary cambium (Rowe and Speck, 2005, Isnard and Silk, 2009), which increases the hydraulic capacity of the stems and available leaf area for photosynthesis in relation to their stem ratio. It was also noted that during growth the vertical juvenile stems of lianoids tended to be stiff and the development of a flexible stem did not occur unless the stems came into contact with the trunk or branches of a host tree and did not reach maturity (Lahaye et al., 2005)). The acquisition of the climbing trait has occurred independently in several plant clades through the acquisition of genes which permanently and irreversibly suppressed the formation of self-supporting trunks. The implication is that lianas including *D. obovata* are dependent on a forest habitat and are not evolved to compete in a grassland environment. Conversely, it can be reasoned that in the absence of contact with trees or bushes, the juvenile stems will remain stiff or semi flexible and it is recorded that *D. obovata* can form bushes of several metres in height (Coates Palgrave, 1977).

Besides the confirmation of the dispersal of *D. obovata* diaspores by wind (Chapter 3) two other aspects of lianoid propagation were confirmed by the mapping of individual plants in large dense stands in the two urban nature reserves. These were the clonal reproduction of plants from the rooting of lateral branches or runners in contact with the soil and the production of adventitious shoots or suckers from shallow lateral roots. It has been noted that although individual genets of clonally reproducing plants follow the $^{-2}/_{3}$ self thinning rule, it does not apply to physiologically integrated ramets of the same plant (Hartnett and Bazzaz, 1983). This then provided an explanation for the ability of *D. obovata* to form large dense stands which effectively exclude other plant species.

The results of the wind dispersal modelling and history of establishments indicates that although long distance diaspore dispersal is possible, the successful establishments at the two survey sites at Marian Wood Nature Reserve were infrequent and occurred at an average rate of one establishment every 5.6 years. This could indicate that *D. obovata* seeds have a very low germination rate in the grasslands or that the seedlings may not be able to compete very well against grass species especially where a closed grass canopy is present (D'Onofrio et al., 2015). The wind dispersal model (Chapter 3) is simplistic and was developed for the primary purpose of confirming if there was a critical maximum distance from the edge of the canopy in order for successful diaspore dispersal to take place. It was estimated that this distance was 1.5m but varied according to a combination of the gradient and shape of the canopy and wind strengths. The model does not account for the effects of wind turbulence, vortex shedding and storm events (Cain et al., 2000, Nathan et al., 2002, Soons., et al., 2004, Tackenberg et al., 2003), which can greatly extend the range of seed dispersal and explains the presence of *D. obovata* recorded throughout the grasslands in some of the study areas (Chapter 2) which were further than 100m from the forest. The percentage of *D. obovata plants* situated within 1.5m of the edge of the canopy was not assessed as part of this study and an estimation of the annual number of establishments for any given length of the forest canopy was not performed. However the mapping of *D. obovata* distribution in four nature reserves (Chapter 2) did record very high densities of *D. obovata* in the forest canopies between 1:64m^2 – 1:400m^2 in the centre of the forests to 1:16m^2 – 1:64m^2 on the forest fringes (Chapter 2) and the frequency of *D. obovata* mapped on the fringes of the forests in Roosefontein Nature Reserve and the Westville Campus grasslands suggests that successful establishments have occurred on numerous occasions during the time period for which historical GIS data was available.

4.2 Conclusion

It was confirmed that *D. obovata* is primarily distributed through wind dispersed diaspores and that in order to successfully disperse beyond the forest boundaries into adjacent grasslands *D. obovata* diaspores needed to be released from a position close to the canopy edge the exact distance depending on a combination of canopy shape and wind strengths. *D. obovata* establishments within the grasslands were infrequent in relation to any particular parent plant and could be attributed to competition for resources between seedlings and grasses. Once *D. obovata* plants were successfully established in the grasslands the plants had an inherent competitive advantage over grass species through clonal propagation of adventitious roots and

rooting of lateral branches which enable the plant to expand its canopy area at a continuous rate. The process of self thinning through canopy contact mortality was avoided since all plants within any single stand were in fact ramets of a single plant. Once established in the grasslands *D. obovata* was not effectively controlled through historic bush encroachment management practices and only the manual clearing and treatment with a herbicide was successful. A correlation between large herbivores and the lack of *D. obovata* was identified but the relationship is not understood. Finally, *D. obovata* could no longer be considered as occurring in only forest or woodland habitats and in the absence of large herbivores has successfully encroached into the moist coast grasslands of the reserves of eThekwini Municipality and represents a further threat to this already threatened grassland habitat.

4.3 Challenges and future research requirements

A number of shortcomings were identified in the understanding of *D. obovata* and its encroachment into moist coast grasslands and which would benefit from further investigation. The first is that the phenology of *D. obovata* is unknown and the plant seems to have been taken for granted as just being part of the forest habitat despite it occupying a large portion of that habitat. The second is that the notion that plants that have evolved to occupy specialist niches and are restricted to the habitat or environment in which they have evolved has been challenged. This raises a question regarding the potential for plants previously considered as specialised to use the traits that provide them with a competitive advantage in their preferred habitat to exploit available opportunities in modified ecosystems such as fragmented landscapes where new niches are provided or alternatively where competition for resources or agents that suppress their germination or growth have become absent. The third shortcoming is the lack of information pertaining to the germination rates of *D. obobata* seed in the field and what conditions are required for successful germination to occur. The final question that requires further investigation is the relationship between *D. obovata* and large mixed feeder herbivores where the actual mechanism for the suppression of *D. obovata* has not yet been identified. Whether or not mixed feeders suppress the ability of *D. obovata* to compete against grasses at the seedling stage or if they forage on adult plants is unknown. This needs to be confirmed together with the stocking ratios required to control *D. obovata* in the grasslands for the effective management of threatened moist coast grasslands by reserve managers.

14.4 References

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